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# A Revision of the Bees of the Genus *Andrena* of the Western Hemisphere



Part XIV

Subgenus *Onagrandrena*

Wallace E. LaBerge and Robbin W. Thorp

Part XV

Subgenus *Hesperandrena*

Robbin W. Thorp and Wallace E. LaBerge

Illinois Natural History Survey Bulletin  
Volume 37, Articles 1 and 2  
March 2005

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## INTRODUCTION

The subgenus *Onagrاندrena* was first recognized and described by Linsley and MacSwain (1956) to include those black *Andrena* that are oligolectic on plants of the family Onagraceae and have pollen-collecting hairs modified to collect the specialized pollen from those plants. The males are more difficult to recognize than the females and most males are very similar to those of *Melandrena*. Since first described, two species of *Onagrاندrena* have been recognized that have pale vestiture in both sexes. However, the pollen collecting hairs of both of these are of the *Onagrاندrena* type, both sexes have well-formed pronotal angles and lateral ridges, and the males have relatively narrow, long mandibles with reduced or absent subapical teeth.

The species of *Onagrاندrena* are very similar and are difficult to tell apart. Populations seem to be relatively isolated in desert locations with habitats amenable to the host plants. This, we believe, has led to a proliferation of species and we can detect slight average differences between populations from different geographic locations within some species. A few of these microgeographic races have been recognized in the literature as subspecies, but the present authors prefer not to formally recognize these races with names.

The reader is referred to earlier sections of this revision (LaBerge 1967, 1969, 1971, 1973, 1977, 1980, 1986, 1989; LaBerge and Bouseman 1970, 1987; LaBerge and Ribble 1972, 1975; Bouseman and LaBerge 1979; Thorp, 1969; Donovan, 1977) for details of morphology and for a more complete bibliography of the literature on *Andrena*. No new morphological terms have been introduced in the present work and the bibliography presented includes only references cited in the text or not listed in earlier parts of the revision. Published locality and floral records are included in the appropriate sections near the end of each species account. Maps showing the known distributions of species (Figs. 2-6) do not have all listed localities spotted on them. Localities that could be located only in a general way, such as county, or could not be found on maps or in gazetteers are omitted.

Considerable detailed information is available concerning the floral activity of several species of *Onagrاندrena* in papers by Linsley, MacSwain, Raven and Thorp (1963a and b, 1964) and MacSwain, Raven, and Thorp (1973). These papers also provide brief notes on nesting burrows and an earlier paper by Linsley, MacSwain and Smith (1955) gives details on the nesting biology of a few species of *Onagrاندrena*.

Institutions in which type material is deposited are listed with contractions as follows:

AMNH—American Museum of Natural History, New York City

CAS—California Academy of Science, San Francisco

INHS—Illinois Natural History Survey, Champaign

LACM—Los Angeles County Museum (of Natural History), Los Angeles

PANS—Philadelphia Academy of Natural Sciences

USNM—United States National Museum (of Natural History), Washington, D.C.

UCB—University of California at Berkeley (Entomology Collection)

UCD—University of California at Davis (Entomology Collection)

UCR—University of California at Riverside (Entomology Collection)

UKL—University of Kansas, Lawrence

USU—Utah State University, Logan

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**Subgenus ONAGRANDRENA Linsley and MacSwain**

*Onagrarendra* Linsley and MacSwain, 1956, Pan-Pacific Ent., 32: 111-112; Lanham, 1949, California Univ. Publ. Ent., 8:183-238; Mitchell, 1960, North Carolina Agr. Exp. Sta. Tech. Bul. 141:86-257; LaBerge, 1964, Univ. Nebraska St. Mus. Bul. 4:315; 1986, Trans. American Ent. Soc., 111:441-458.

*Onagrarendra* are moderately large to large bees with short malar spaces, short to moderately tall vertices (rarely taller than half an ocellar diameter above lateral ocellus), and genal areas of moderate width (broad in males with long mandibles). Both sexes usually have the propodeum outside of the dorsal enclosure punctatorugose and the enclosure moderately rugulose. The females have the propodeal corbiculum not at all developed. The hairs along the upper and posterior margin of the propodeum are long and plumose but do not form a long overhanging margin to a basket and these long hairs grade into the shorter internal plumose hairs. The scopal hairs are long, relatively sparse to extremely sparse and simple. Both sexes lack tergal pale fasciae and most males lack sternal subapical pale fimbriae.

**Common Characters.** Medium-sized to large bees; facial quadrangle quadrate to slightly elongate; eyes with inner margins parallel or converging slightly towards mandibles; clypeus black, punctate; vertex above lateral ocellus usually equals one ocellar diameter or less; genal area usually broader than eye in profile; galea usually broad with apicolateral margin concave, a few species with small straight-sided galeae, usually galea exceeded by last two maxillary palpal segments; labral process entire to bidentate, usually recurved. Pronotum usually without humeral angle or lateral ridges but present in four species. Posterior hind tibial spur not broadened basally or twisted in outer third. Pterostigma not especially narrow usually slightly wider than from inner margin prestigma to anterior wing margin; three submarginal cells usually present; vein 1st m-cu usually meets second submarginal cell near middle of cell or beyond middle; vannal lobe hind wing broad, excision deep. Propodeal enclosure usually irregularly rugulose, smooth or nearly so in a few species; surfaces outside of enclosure with distinct to coarse punctures, often separated only by narrow, sharp ridges, smooth in several species. Vestiture variable but often black in large part, without pale apical tergal fasciae.

**Female.** Facial foveae shallow, large, separated from lateral ocellus by half to one ocellar diameter, usually extending down to below a line at lower margins of antennal fossae; subgenal coronet present. Propodeal corbícula absent or poorly expressed; without long plumose hairs anteriorly, dorsally with long plumose straight hairs, internally with abundant plumose hairs short below and grading into upper long hairs; trochanteral flocculus complete but weak; tibial scopal hairs long to extremely long, moderately abundant to sparse, simple.

**Male.** Mandible short to elongate, apposite to decussate; antenna moderately long, first flagellar segment slightly shorter than second segment to slightly but distinctly longer. Sterna usually without subapical fimbriae; with apical lobe distinctly bidentate; sternum 8 usually with apex capitate and distinctly separated from neck region; neck region and often apical lobe more or less hairy.

## PHYLOGENY

The *Onagrاندrena* probably arose from a common ancestor with the subgenus *Andrena*. Only a few morphological changes (shortened malar space, loss of propodeal corbiculum, and shortened vertex) are needed to separated the generalized *Onagrاندrena* from generalized *Andrena*. Few additional changes (color of the vestiture, simplified trochanteral flocculus, and coarse sculpturing of the propodeum) are needed to account for the majority of species of *Onagrاندrena*. The Eurasian fauna does not have any species belonging in this subgenus or approaching this combination of characteristics, so we assume it to have evolved in western North America where it exists at present.

The accompanying phylogenetic diagram (Fig. 1) showing the hypothetical relationships among the known species of *Onagrاندrena* is based on 22 attributes listed below in both apomorphic and plesiomorphic states (Table 1). The tree is rooted by a hypothetical ancestor based on comparing situations in the subgenus *Andrena s. str.* and in more generalized bees (Halictidae and Colletidae) and coded "0" for all states. A parsimony analysis of the data set (Appendix 1) using David Swofford's PAUP\* 4.0b8 program (2002 Sinauer Associates, Sunderland, MA), yielded 200 minimum-length trees, of which the strict consensus is shown in Figure 1. This tree indicates that the four species with distinct pronotal humeral angles and lateral ridges in both sexes could possibly be considered as a separate subgenus. This tree indicates that the four species with distinct pronotal humeral angles and lateral ridges in both sexes could possibly be considered as a separate subgenus. These four,



however, do not show any apomorphic characteristics that are not present in some or all of the remaining *Onagrarendra* species and the present authors prefer to recognize them as the most generalized species of the *Onagrarendra*.

Table 1. A list of the plesiomorphic and apomorphic alternatives of the characters upon which our phylogenetic study was based.

Plesiomorphic	Apomorphic
1. Pronotum with humeral angles and lateral ridges	without angles or ridges.
2. Propodeal enclosure weakly sculptured	coarsely sculptured.
3. Female vestiture entirely pale	largely or entirely black.
4. Propodeum with distinct dorsal surface	declivous from base.
5. Dorsal thoracic hairs long	short.
6. Wing membranes hyaline or weakly infumate	deeply infumate.
7. Labral process with apical portion broad, sides straight or shape triangular	narrow, sides concave.
8. Metasomal terga black without metallic blue or violaceous reflections	terga with metallic blue or violaceous reflections.
9. Propodeum outside of enclosure finely rugulate and/or tessellate, not punctatorugose but punctate	finely to coarsely punctatorugose.
10. Female clypeal punctures dense	punctures sparse.
11. Galeae normal, dulled by fine dense tessellation	small, shiny.
12. Scutellar punctures separated by half a puncture width or more	punctures dense.
13. Female terga 2 and 3 with apical areas punctate at least basally	apical areas impunctate.
14. Female hind tibial scopal hairs dense, obscuring surface	long, sparse, not hiding surface.
15. Ocelli not enlarged	ocelli more or less enlarged.
16. Vertex above lateral ocellus equals one ocellar diameter	equals less than one ocellar diameter.
17. Lower mesepisternum punctate	punctatorugose.
18. Male mandible with subapical tooth	without subapical tooth.
19. Male tergal vestiture entirely pale	dark on terga 6 and 7 or mostly dark.
20. Male thoracic hairs entirely to partly pale	entirely dark.
21. Male flagellar segment one equal to or only slightly longer than segment 2	distinctly longer than segment 2 and often longer than segment 3.
22. Male genal area broad, about one and one-half times as broad as eye	genal area not much broader than eye in profile.

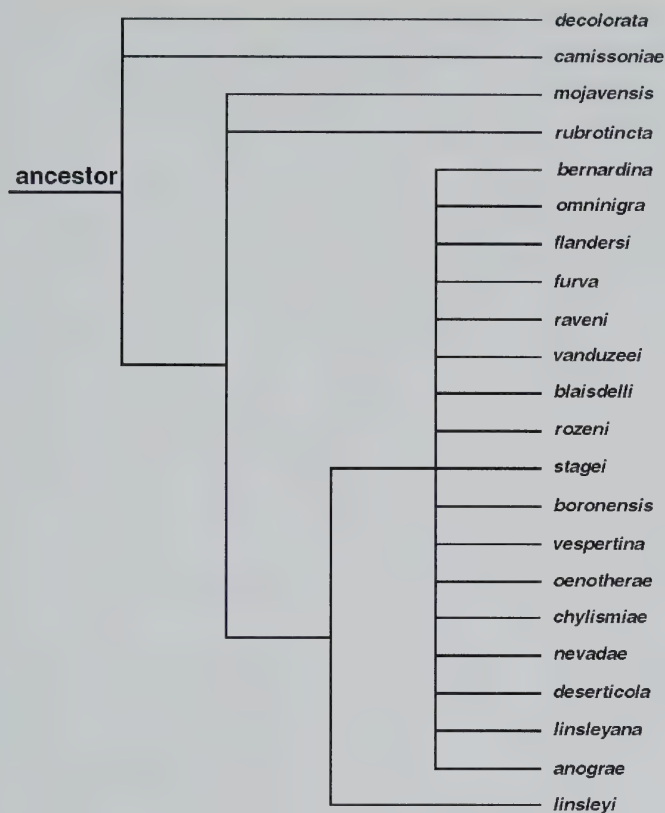


Fig. 1. Phylogenetic diagram of the species of the subgenus *Onagrاندrena*. This is a strict consensus tree of 200 most parsimonious trees all of length 45 with consistency index + 0.489 and retention index = 0.720. Diagram derived by use of PAUP\* 4.0b8 of D. L. Swofford (2002). Note that the majority of the tree is unresolved due to the small number of characters available. The authors thank Phil Ward of the University of California-Davis for running the program to produce this diagram.

## BIOLOGY

The subgenus *Onagrاندrena* is defined in large measure by a suite of behavioral, morphological, and physiological traits associated with collection of pollen by the female bees from a few closely related, usually congeneric, species of the the plant family Onagraceae. This behavior, referred to as oligolecty (Linsley 1958), is accompanied by morphological adaptations of the female pollen transport apparatus. The females have sparse unbranched (simple) scopal hairs, they lack propodeal corbiculae, and they have poorly formed trochanteral flocculi on the hind legs (trochanters). These three structural modifications make the pollen transport apparatus well adapted to handle and store large triangular pollen grains that are tied together in webby masses by viscin threads (Linsley 1958, Thorp 1979, Skvarla *et al.* 1978). P.H. Timberlake was one of the first to recognize the correlation between the long simple hairs of the scopa in *Andrena* and the collection of pollen from Onagraceae according to Cockerell (1937). Females of this subgenus also have predominantly black integument and black, dark brown or ochraceous vestiture that enhances absorption of radiant energy. This is advantageous for foraging flights during low light, cool matinal or crepuscular periods when many of the host plants present pollen. In addition to coincidental daily rhythms, these annual spring-flying bees exhibit seasonal synchrony with bloom of



their pollen host plants. In some species this appears to include abilities to refrain from emerging in unfavorable years and to emerge early (e.g., in late autumn) when their host plants are stimulated to germinate early by aseasonal heavy summer rains. Thus, loss of pollen host plants and/or habitat due to urbanization and agriculture diminishes populations of bees.

**Distribution and Abundance.** Bees of the subgenus *Onagrاندrena* are limited to the western United States and northwestern Mexico west of the 105th meridian and between the 42nd and 35th parallels. All but four species (*anograe*, *linsleyana*, *nevadae*, and *stagei*) occur in California. Nine are restricted to California and four of these (*camissoniae*, *omninigra*, *vanduzeei*, and *vespertina*) occur exclusively in cismontane California, the other five (*bernardina*, *deserticola*, *flandersi*, *furva*, and *mojavensis*) are transmontane or occur in the southern deserts. Four additional species (*blaisdelli*, *boronensis*, *decolorata*, and *oenotherae*) occur primarily in California, but also extend their ranges into Baja California del Norte, Mexico. Several species are severely limited in distribution and/or are known from a very few specimens. Only females are known for *A. nevadae* (2) and *A. stagei* (3). *Andrena camissoniae* and *A. decolorata* are each known from less than 20 specimens and from three to four localities respectively. *Andrena vespertina* is known from nearly 170 specimens, but only from two disjunct localities separated by about 220 air miles.

Bees of the subgenus *Onagrاندrena* tend to occur entirely within the distribution of their pollen host plant taxa. Peripheral populations of Onagraceae tend to be pollinated by generalist bees or other pollinators or have shifted their reproduction to self-compatibility or autogamy. *Andrena linsleyi* occupies only the southern portion (less than half) of the range of *Oenothera deltoides* (Linsley *et al.* 1963a: Fig. 2). *Andrena rozeni* occupies much of the distribution of *Camissonia claviformis*, but does not extend north into Oregon and Idaho with its pollen host, nor as far east as its host in Nevada and Arizona (Linsley *et al.* 1963a: Fig. 1, as *O. clavaeformis*).

Few remnants of presumably more widespread populations of *Onagrاندrena* remain, especially in the Central Valley and coastal areas of California and these are threatened by encroachment of human populations. While they can forage for nectar at flowers of many plants, these bees are restricted to plants of the family Onagraceae for pollen resources necessary to rear their young. Many habitats no longer exist where populations of these bees were found when the studies by E.G. Linsley and J.W. MacSwain were initiated in the mid-1950s. Locations and descriptions of the major habitats where most of the biological studies on bees of the subgenus *Onagrاندrena* have been conducted are provided by E.G. Linsley and his colleagues (Linsley *et al.* 1963a, b, 1964, 1973; MacSwain, *et al.* 1973). Relevant features of the Onagraceae host plants are provided by P.H. Raven in the same series of publications as well as in Raven 1962, 1964, 1969. Information on *Clarkia* is available in the monograph by Lewis and Lewis (1953) and on *Gayophytum* by Lewis and Sweykowski (1964).

**Overwintering, Emergence, and Seasonal Flight.** Adults of most California species fly in spring, primarily in March and April. However, species oligolectic on *Clarkia* (*A. bernardina*, *omninigra*) and *Gayophytum*, and *A. vanduzeei* are active principally in late spring (May and June) and early summer (June and July) respectively. Species that occur primarily in the Colorado Desert (*A. linsleyi*, *rozeni*, *rubrotincta*) emerge as early as February (Linsley *et al.* 1963a). Those that live in the Great Basin (*A. anograe*, *chylismae*, *linsleyana*, *nevadae*, *raveni*, *stagei*) fly primarily from May into July (Linsley *et al.* 1963b, Thorp 1987).

Linsley *et al.* (1963a) list apparently anomolous early records for three species that occur in the Colorado Desert of California (*rozeni*, *linsleyi*, and *rubroincta*). These species usually first appear in February, but males of each were collected between 27 November and 17 December 1921 at Needles, California. The authors suggested that the most likely reason for these early records was an unusual season. Precipitation records (US Weather Bureau 1921) for July through December 1921 show that the Needles, California station received above normal rainfall for the months of August, September, October, and December in 1921. Rainfall in just August and September was 4.66 inches above normal and nearly an inch higher than the normal for the entire year at Needles that year. We have no information about whether the pollen host plants of these bees bloomed in response to these unusually high, aseasonal rains, but the following example of a southeastern California desert oligolege and its host plant is strongly suggestive.

Hurd (1957) reported collecting specimens of the normally spring flying melittid bee, *Hesperapis fulvipes* Crawford, in October 1951 in the eastern Mojave and Colorado deserts of California. This occurred after unusual heavy summer rains that caused the pollen host plant of the bee, *Geraea canescens*, to bloom several months ahead of time. Precipitation records (US Weather Bureau 1951) for July through December 1951 at three stations in southeastern California (Needles, Blythe, and Parker Reservoir) confirm that they all received heavy rains in August 1951 (3.47 to 5.52 inches above normal). This case combined with weather data for 1951, demonstrates that heavy August rain was sufficient to stimulate aseasonally early emergence of the oligolectic bee and bloom of its pollen host plants. The similar aseasonal heavy rainfall pattern in 1921 thus offers an explanation for the early appearance on *Onagrاندrena* at Needles that year.

Seasonal flight patterns of the bees are closely tied to the bloom seasons of their pollen host plants. It is well known that many plants have the ability to hold over inclement years as seed investment in the soil. This is particularly striking in desert plants and gives rise to spectacular bloom years when preceding fall rains have been adequate to cause germination of much of the seed bank at one time. There is evidence to suggest that at least some *Onagrاندrena* survive inclement years and emerge a year or more later, "... although ... this adaptation may not be a perfect one ..." (Linsley *et al.* 1963a). *Andrena mojavensis* appears to be adapted to remain more than one year in its brood cells when conditions are unfavorable and to emerge when conditions become favorable. In the poor flower year of 1959, small numbers of females were concentrated on the few flowers available. In 1960, both flowers and bees were extremely abundant. The high population of bees in 1960 was not likely to have been produced by the previous generation alone (Linsley *et al.* 1964).

Linsley and MacSwain (1963) report that adults of *A. (O.) oenotherae* (as *oraria*) were excavated from nest cells in early October and early February, indicating that this species and presumably other spring flying *Onagrاندrena* overwinter as adults in their brood cells (Linsley *et al.* 1963a). Some *Onagrاندrena* appear to be protandrous: *A. rozeni*, *linsleyi* (Linsley *et al.* 1963a).

**Male Behavior.** Males of *A. rozeni* characteristically and consistently over various localities in the Colorado Desert of California appeared about two hours before sunset in the vicinity of the female pollen host plant, *Camissonia claviformis* (Linsley *et al.* 1963a). This was about 30 minutes before females began foraging for pollen. Males flew rapidly at the height of the flowers, approaching, but not contacting pollen collecting females. Copulation was only observed with females that were freshly emerged and had not yet begun to collect pollen. Males are rarely seen at other times of day.

Males of *A. linsleyi* visit Asteraceae: *Geraea canescens* and *Palafoxia linearis* in the AM for nectar and seeking females in some years. When the female pollen host, *Oenothera*



*deltoides*, is the major source of nectar, male activity is concentrated on it. Most copulation records involve other flowers, however. Male flight among flowers appears erratic when compared to the more regular flight of *A. rozeni* males.

**Nests-Sites, Architecture, and Construction.** Nests of only a few species of *Onagrarendra* have been excavated and described including: *A. rozeni* and *A. linsleyi* (Linsley *et al.* 1963a); *A. raveni* (Linsley *et al.* 1963b); and *A. mojaviensis*, *A. deserticola*, and *A. boronensis* (Linsley *et al.* 1964). Nests were also excavated for *A. oenotherae* (as *oraria*) (Linsley and MacSwain 1963), but no information on nest architecture was provided.

Females of these bees most frequently nest in sandy soil. Nests are often initiated in shallow depressions and tend to be scattered, but small aggregations were noted for *A. deserticola*. They range in depth from about 36 cm to over 1 m. The entrance shaft is often vertical (*A. linsleyi*, *raveni*, *mojaviensis*, and *deserticola*) but may angle downwards at 45 degrees for the first 5–14 cm as in *A. rozeni* and *boronensis*.

**Flower Relationships.** Female *Onagrarendra* all exhibit host-specificity for pollen (oligolecty) with members of the Onagraceae (Table 2). Females of 15 of 22 species of *Onagrarendra* collect pollen from species of *Camissonia*. Females of four species collect pollen from *Oenothera*. Females of two species collect pollen from *Clarkia* and the remaining one collects pollen from *Gayophytum*. Based on seasonal and diurnal synchrony, fidelity of female bees foraging for pollen host plants, numbers of individual bee foragers, and their size and fit with their host floral structures, these bees are probably the principal pollinators of their host species of Onagraceae except for *Oenothera*.

The long viscin threads in *Oenothera* tie many pollen grains together in long strands and are an adaptation to pollination by hawkmoths. These long loose strands of pollen hang from the venters of the moths and become draped over the lobes of the stigma as the pollinators hover in front of the flowers probing for nectar. This presents a handling problem to most female bees that attempt to pack pollen in their pollen transport structures (Thorp 1979). Females of *Onagrarendra* have solved this problem by simplifying their pollen transport structures. Females of most generalist bees are unable to effectively cope with the largest and webbiest pollen grains of the Onagraceae. The pollen transport apparatus of the honey bee, *Apis mellifera* L., is particularly ill-suited for packing pollen of *Oenothera* (Linsley *et al.* 1963a). These flowers are usually nocturnal blooming, adapted for hawkmoth pollination, and possess the largest and webbiest grains (Greggory 1963–64, Raven 1979, Skvarla *et al.* 1978, Linsley *et al.* 1963a). Females of four species of *Onagrarendra* (*anograe*, *linsleyana*, *linsleyi*, and *stagei*) that collect pollen from *Oenothera* have the most sparse scopal hairs. These bees usually collect residual pollen the following morning before the flowers close for the day, for example, *Andrena linsleyi* (Linsley *et al.* 1963a).

Flowers of many of the genera of Onagraceae are well adapted for pollination by bees, especially oligolectic *Andrena* (Linsley *et al.* 1963a, b, Thorp 1969, Linsley *et al.* 1973, MacSwain *et al.* 1973, Estes and Thorp 1974, Raven 1979). In contrast to hawkmoth and hummingbird pollinated Onagraceae, these frequently have viscin threads reduced in length and number, for example *Camissonia*, *Clarkia*, and *Gayophytum* (Linsley *et al.* 1963a, b, Thorp 1969). Skvarla *et al.* (1978) note that structures of the viscin threads are often different between moth and bee pollinated species of the tribe Onagreae.

Most *Camissonia* are matinal flowering and bright yellow, a few are white and crepuscular or nocturnal flowering. Their oligolectic bees therefore forage primarily early in the morning (at or before sunrise) and/or late in the afternoon until sunset. Flowers of *Clarkia* and of *Gayophytum* present pollen most of the day. The female *Onagrarendra* on *Clarkia* forage in the middle of the day. Since *Clarkia* anthers dehisce gradually, pollen foraging



female bees vibrate the anthers to release additional pollen. *Gayophytum* occurs at high elevations and has late summer flowering. Its small flowers are pollinated primarily by small bees and throughout the day, but also by one species of *Onagrandrena*. *Onagrandrena* females gather nectar from a variety of other floral sources, especially when the pollen host is not suitable, for example, *Oenothera* with the nectar at the base of its long hypanthium.

**Pollen Competition.** More than one species of *Onagrandrena* occur together at some localities and some even share the same pollen host plant resources sympatrically (Linsley *et al.* 1963 a, b, 1964, 1973). They also share host plants with some oligolectic species of the subgenus *Diandrena* (Thorp 1969, Linsley *et al.* 1973). How do they manage to coexist in sympatry? Many of the ways have been discussed by Thorp (1969) in relation to coexistence among members of the subgenus *Diandrena*. These include: 1) some do not share the same floral resource where they co-occur; 2) sharing of the same floral resource is not among most closely related species within the subgenus; 3) some seasonal resource division occurs; 4) some diurnal resource division with species with larger and darker females foraging earlier occurs; 5) not all populations of any one species occur in sympatry with the same guilds of other species; 6) species dominance may shift among areas of sympatry.

Table 2. Principal pollen flowers for species of *Onagrandrena*.

<i>anograe</i>	<i>Oenothera caespitosa, albicaulis, scapoidea</i>
<i>linsleyana</i>	<i>Oenothera pallida</i>
<i>omninigra</i>	<i>Clarkia dudleyana, unguiculata, cylindrica, speciosa</i>
<i>bernardina</i>	<i>Clarkia</i> (?)
<i>flandersi</i>	<i>Camissonia campestris, claviformis</i>
<i>furva</i>	<i>Camissonia campestris</i>
<i>oenotherae</i>	<i>Camissonia campestris, cheiranthifolia</i>
<i>vespertina</i>	<i>Camissonia boothii</i>
<i>boronensis</i>	<i>Camissonia crassifolia</i>
<i>stagei</i>	<i>Oenothera</i> (?)
<i>chylismiae</i>	<i>Camissonia claviformis</i>
<i>rozeni</i>	<i>Camissonia claviformia, boothii</i>
<i>linsleyi</i>	<i>Oenothera deltoidea</i>
<i>blaisdelli</i>	<i>Camissonia campestris, bistorta</i>
<i>deserticola</i>	<i>Camissonia campestris</i>
<i>nevadae</i>	<i>Camissonia</i> (?)
<i>raveni</i>	<i>Camissonia claviformis, tanacetifolia</i>
<i>vanduzeei</i>	<i>Gayophytum diffusum</i>
<i>rubrotincta</i>	<i>Camissonia brevipes, claviformis</i>
<i>mojavensis</i>	<i>Camissonia kernensis</i>
<i>camissoniae</i>	<i>Camissonia campestris</i>

Examples of co-occurrence include: West of Blythe, CA—*A. rozeni*, *linsleyi*, *rubrotincta* (Linsley *et al.* 1963a); West of Austin, NV—*A. rozeni*, *raveni*, *chylismiae* (Linsley *et al.* 1963b); Short Canyon, CA—*A. mojavensis*, *boronensis*, *deserticola*, *flandersi* plus two *Diandrena* (Linsley *et al.* 1964); East of Bakersfield, CA—*A. oenotherae* (as *convallaria*), *deserticola*, *vespertina* (Linsley *et al.* 1973); Hungry Valley, CA—*A. blaisdelli*, *deserticola* (Linsley *et al.* 1973); Northeast of Santa Margarita, CA—*A. blaisdelli*, *furva*, *oenotherae* (as *convallaria*), *omninigra*, (Linsley *et al.* 1973). At most of these localities, potential competition for pollen resource is minimized through availability of more than one species

of pollen host plant, and differences in seasonal and diurnal abundance of species foraging on that host.

**Parasites, Predators, and Associates. Strepsiptera: Stylopidae:** The presence of adult *Stylops* between the metasomal tergites has been noted for: *Andrena boronensis* (Linsley *et al.* 1964); *A. chylismae* (including one female as *thorpi*) (Linsley and MacSwain 1962, Linsley *et al.* 1963); *A. linsleyi* (Linsley and MacSwain 1955, Linsley *et al.* 1963); *A. oenotherae* (as *convallaria subhyalina*) (Linsley and MacSwain 1963, Linsley *et al.* 1964); *A. raveni* (Linsley *et al.* 1963); *A. rozeni* (Linsley and MacSwain 1955, Linsley *et al.* 1963); and *A. vespertina* (Linsley and MacSwain 1961). We have found *Stylops* in specimens we have examined of *A. deserticola*, *A. linsleyana*, and *A. raveni*. Up to 67% of one sample of *A. oenotherae* at one site were found to contain *Stylops* (Linsley and MacSwain 1963). Female bees from many sites had up to three *Stylops* and one female *A. oenotherae* from near Ensenada, Baja California del Norte, Mexico, contained four. **Hymenoptera: Anthophoridae:** Females of a species of *Nomada* were noted as being active near burrows of *A. chylismae*, *A. linsleyi*, *A. raveni*, and *A. rozeni* (Linsley *et al.* 1963), and of *A. boronensis* and *A. deserticola* (Linsley *et al.* 1964). **Diptera: Asilidae:** Robber flies, *Callinicus calcanus* (Loew), were recorded as predators on *A. omninigr*a by Linsley (1972).

# KEY TO THE FEMALES OF ONAGRANDRENA

1. Pronotum with humeral angle and blunt vertical ridge laterally (Fig. 18);  
propodeal dorsal enclosure weakly sculpture ..... 2.
- Pronotum without humeral angle and ridge (Fig. 15); propodeal  
enclosure coarsely rugulate or coarsely punctate ..... 5.
- 2(1). Vestiture entirely pale, yellow to ochraceous ..... 3.
- Vestiture all or mostly black, at most dorsum of thorax and vertex with pale  
hairs and these usually dark ochraceous or fulvous ..... 4.
- 3(2). Propodeum declivous, without distinct dorsal surface, areas outside of  
enclosure evenly tessellate with scattered puncture .....  
..... *Andrena decolorata* LaBerge and Thorp.
- Propodeum with dorsal surface, area outside of enclosure with weak  
irregular rugulae as well as punctures and tessellation (Fig. 21) .....  
..... *Andrena camissoniae* Linsley and MacSwain.
- 4(2). Mesoscutum at least posteromedially and scutellum shiny, at least in part  
unshagreened .....  
..... *Andrena mojaviensis* Linsley and MacSwain.
- Mesoscutum dulled by fine shagreening throughout or shiny only  
in very small posteromedial area; scutellum dull, finely shagreened  
throughout ..... *Andrena rubrotincta* Linsley.
- 5(1). Most dorsal thoracic hairs shorter than width of scape (a few to  
several longer hairs may be present), velvetlike in appearance ..... 6.
- Most dorsal thoracic hairs at least as long as scape width and usually  
longer, not at all velvetlike ..... 9.
- 6(5). Wing membranes infumate, brown to almost black ..... 7.
- Wing membranes scarcely, if at all, infumate, hyaline ..... 8.

- 7(6). Labral process with apical portion about as broad as base of scape; vertex above lateral ocellus equals about one ocellar diameter ..... *Andrena bernardina* Linsley.  
 Labral process with apical portion long, narrower than base of scape; vertex above lateral ocellus equals more than one ocellar diameter ..... *Andrena omninigra* Viereck.
- 8(6). Terga 2 and 3 with apical area impunctate medially; mesoscutum with punctures large, deep, surface shiny at least posteromedially ..... *Andrena flandersi* Timberlake.  
 Terga 2 and 3 with apical areas punctate at least in basal half across entire tergum; mesoscutal punctures small, crowded, surface dull, shagreened ..... *Andrena furva* Linsley and MacSwain.
- 9(5). Dorsal thoracic hairs dark brown to black ..... 10.  
 Dorsal thoracic hairs pale, ochraceous to fox-red ..... 23.
- 10(9). Metasomal terga black with distinct violaceous to blue reflections ..... *Andrena raveni* Linsley and MacSwain.  
 Metasomal terga black, violaceous reflections absent or faint ..... 11.
- 11(10). Mesoscutum dulled by fine dense shagreening ..... 12.  
 Mesoscutum shiny, unshagreened except at extreme periphery..... 21.
- 12(11). Propodeum outside of enclosure finely, irregularly rugulate and/or tessellate, not punctatorugose or only finely so; mesepisternum with distinct punctures, not punctatorugose ..... 13.  
 Propodeum outside of enclosure and mesepisternum moderately to coarsely punctatorugose ..... 15.
- 13(12). Clypeal punctures relatively sparse, separated mostly by half to one puncture width, median impunctate line usually complete; labral process usually triangular with straight sides and rounded tip ..... *Andrena linsleyi* Timberlake.  
 Clypeal punctures dense, separated by half a puncture width or less, impunctate line usually incomplete or absent, rarely complete and extremely narrow; labral process with apical part narrowed, sides concave, or broad and bidentate apically ..... 14.
- 14(13). Lateral ocellus separated from facial fovea by one ocellar diameter or Lateral ocellus separated from facial fovea by about half an ocellar diameter; terga 3 and 4 without metallic reflections ..... 22.
- 15(12). Galeae small, shiny, unshagreened or only slightly shagreened near tips; tergum 1 with basal area shiny, unshagreened ..... *Andrena blaisdelli* Cockerell.  
 Galeae longer, dulled by fine dense shagreening; tergum 1 with basal area at least lightly shagreened ..... 16.
- 16(15). Scutellar punctures relatively sparse (especially in anterior third), spaces tessellate..... *Andrena rozeni* Linsley and MacSwain (in part).



- Scutellar punctures dense, separated by half a puncture width or less,  
often with interpunctural spaces lacking, punctatorugose ..... 17.
- 17(16). Terga 2 and 3 with apical areas with punctures separated mostly by 3 to  
5 puncture widths..... 18.  
Terga 2 and 3 with apical areas with punctures separated mostly by 1 to  
3 puncture widths ..... 19.
- 18(17). Hind tibial scopal hairs long, sparse, scarcely hiding surface  
..... *Andrena stagei* Linsley and MacSwain.  
Hind tibial scopal hairs shorter, dense, partially obscuring surface  
..... *Andrena boronensis* Linsley and MacSwain.
- 19(17). Tergum 2 with median third of basal area with punctures separated mostly  
by half a puncture width or less .....  
..... *Andrena vespertina* Linsley and MacSwain.  
Tergum 2 with median third of basal area with punctures slightly sparser,  
separated largely by half to one puncture width ..... 20.
- 20(19). Hind tibial scopa with moderately abundant, long, simple hairs, surface of  
tibia somewhat obscured by hairs.....  
..... *Andrena oenotherae* Timberlake.  
Hind tibial scopa with sparse, long, simple hairs not at all obscuring  
surface of tibia (slightly larger bee, slightly sparser scopal hairs,  
slightly darker wings) .....  
..... *Andrena chylismiae* Linsley and MacSwain.
- 21(11). Scopal hairs long, sparse; propodeal enclosure coarsely reticulorugose  
(Fig. 16); terga 2-4 with basal area punctures coarse, deep,  
abundant..... *Andrena nevadae* Linsley and MacSwain.  
Scopal hairs moderately long and dense; propodeal enclosure  
usually shallow, relatively sparse.....  
..... *Andrena deserticola* Timberlake.
- 22(14). Large bees with ocelli distinctly enlarged; lateral ocellus about as broad as  
vertex above it; mesosomal vestiture black; scutellum dull, not shiny  
anteriorly..... *Andrena linsleyana* Thorp.  
Usually smaller bees with ocelli not enlarged; lateral ocellus width narrower  
than vertex above it; mesosoma usually with some vestiture pale  
dorsally, scutellum moderately shiny .....  
..... *Andrena anograe* Cockerell (in part).
- 23(9). Lower mesepisternum punctate, interpunctural spaces tessellate; scutellum  
with anterior punctate area shiny, not tessellate; clypeal punctures  
small, dense..... *Andrena anograe* Cockerell (in part).  
Mesepisternum largely coarsely punctatorugose, lower-posterior area  
punctate, but obscured by dense tessellation; scutellum with anterior  
punctate area dulled by fine tessellation; clypeal punctures larger,  
slightly sparse..... *Andrena rozeni* Linsley and MacSwain (in part).

# KEY TO THE MALES OF ONAGRANDRENA

1. Pronotum with humeral angle and verticle ridge laterally (Fig. 14) ..... 2.  
Pronotum without humeral angle or verticle ridge laterally..... 5.
- 2(1). Mandible without subapical tooth, represented by slight angle not a  
distinct tooth (Fig. 13) ..... *Andrena rubrotincta* Linsley.  
Mandible with distinct subapical tooth (Fig. 22) ..... 3.
- 3(2). Scutellum and mesoscutum dull, shagreened ..... 4.  
Scutellum shiny, mesoscutum shiny at least posteromedially.....  
..... *Andrena mojaviensis* Linsley and MacSwain.
- 4(3). Propodeum outside of enclosure punctatorugose or with distinct fine  
rugulae, dorsal enclosure finely to coarsely rugulose throughout  
..... *Andrena camissoniae* Linsley and MacSwain.  
Propodeum outside of enclosure tessellate with sparse punctures,  
without rugulae, dorsal enclosure tessellate often with short, fine  
rugulae near base (Fig. 25) ... *Andrena decolorata* LaBerge and Thorp.
- 5(1). Mesoscutum and scutellum shiny, interpunctural spaces not shagreened  
except lightly, especially peripherally ..... 18.  
Mesoscutum and scutellum dull, spaces shagreened ..... 6.
- 6(5). Tergal vestiture entirely pale in color or almost so ..... 7.  
Tergal vestiture with dark hairs at least on terga 6 and 7, usually mostly  
entirely black ..... 8.
- 7(6). Mesepisternum and propodeum punctatorugose ..... 19.  
Mesepisternum and propodeum with discrete punctures and small but  
distinct interpunctural spaces..... *Andrena linsleyi* Timberlake.
- 8(5). Thoracic hairs entirely black or dark brown ..... 9.  
Thoracic hairs not entirely dark, mesoscutum with pale hairs at least  
peripherally, usually entirely or mostly pale ..... 10.
- 9(8). Propodeum outside of dorsal enclosure and scutellum punctatorugose;  
propodeal enclosure strongly rugose; ocelli of normal size .....  
..... *Andrena chylismiae* Linsley and MacSwain.  
Propodeum outside of dorsal enclosure not punctatorugose, finely  
sculptured; scutellum with distinct punctures separated by more  
than half a puncture width; propodeal enclosure rugulose; ocelli  
enlarged ..... *Andrena linsleyana* Thorp.
- 10(8). Metasomal terga black with relatively strong metallic blue or purple  
reflections on terga 2 to 5; mesoscutal vestiture entirely pale .....  
..... *Andrena raveni* Linsley and MacSwain.  
Metasomal terga black without metallic reflections or extremely weakly  
violaceous on terga 3- or 4-5; mesoscutal vestiture dark postero-  
medially ..... 11.

- 11(10). Mesoscutum and scutellum with black or dark brown hairs mixed with pale hairs posteromedially or forming a distinct dark patch..... 12.  
 Mesoscutum and scutellum with hairs pale, white to ochraceous ..... 13.
- 12(11). Vertex above lateral ocellus equals slightly more than one ocellar diameter; wings deeply infumate ..... *Andrena omninigra* Viereck.  
 Vertex above lateral ocellus equals one ocellar diameter or less; wings variable, clear to moderately infumate ..... 16.
- 13(11). Clypeal hairs all or mostly pale, ochraceous or white ..... 14.  
 Clypeal hairs entirely black or pale apically only ..... 15.
- 14(13). Scutellum with distinct punctures; facial hairs entirely white or almost so, a few dark hairs may be present near inner eye margin or just below vertex ..... *Andrena rozeni* Linsley and MacSwain.  
 Scutellum punctatorugose; facial hairs between clypeus and vertex black or dark brown at least in large part ..... 17.
- 15(13). Propodeum outside of dorsal enclosure and mesepisternal surface coarsely punctatorugose (Fig. 10); lower mesepisternal surface punctatorugose..... *Andrena oenotherae* Timberlake.  
 Propodeum outside of dorsal enclosure and mesepisternum finely sculptured, not punctatorugose, usually with distinct punctures (Fig. 7); lower mesepisternal surface punctate with punctures separated by one to two puncture widths, interpunctural surfaces shagreened .....  
 ..... *Andrena anograe* Cockerell.
- 16(12). Terga 3–5 or 4–6 with weak metallic reflections; mesepisternum posteromedially and scutellum shiny ..... *Andrena vanduzeei* Linsley.  
 Terga without metallic reflections; mesepisternum and scutellum dull, shagreened or tessellate ..... *Andrena bernardina* Linsley.
- 17(14). Tergum 2 with basal area sparsely punctate, punctures separated mostly by 3 to 5 puncture widths or more; pleura usually with some white hairs ..... *Andrena boronensis* Linsley and MacSwain (in part).  
 Tergum 2 with basal area more densely punctate, punctures usually separated by 1 to 2 puncture widths or less; pleural hairs black .....  
 ..... *Andrena vespertina* Linsley and MacSwain.
- 18(5). Metasomal terga 2 and 3 with apical areas impunctate .....  
 ..... *Andrena flandersi* Timberlake.  
 Metasomal terga 2 and 3 with apical areas minutely punctate at least in basal half ..... *Andrena deserticola* Timberlake.
- 19(7). Metasomal tergum 2 sparsely punctate, punctures separated by 3 to 5 diameters; galea of normal size, shagreened at least basally; face with black hairs along inner eye margins .....  
 ..... *Andrena boronensis* Linsley and MacSwain (in part).  
 Metasomal tergum 2 densely punctate, punctures separated by less than one diameter; galea small, shiny, unshagreened; face without black hairs along inner eye margins ..... 20.



- 20(19). Vertex above lateral ocellus usually equals slightly less than two ocellar diameters, never more, surfaces shiny; flagellar segment long, distinctly longer than segment 2 and usually longer than 3; sterna 2–5 with weak subapical fimbriae of long plumose hairs ..... *Andrena blaisdelli* Cockerell.
- Vertex above lateral ocellus equals more than one ocellar diameter, never less; flagellar segment 1 about as long as segment 2 and never as long as segment 3; sterna 2–5 with narrow subapical fimbriae of short plumose hairs ..... *Andrena furva* Linsley and MacSwain.

## SPECIES ACCOUNTS

*Andrena (Onagrarendra) anograe* Cockerell

*Andrena anograe* Cockerell, 1901, Canadian Ent., 33:154; 1934, American Mus. Nov., No. 697, p. 2.

*Andrena (Melandrena) anograe*: Lanham, 1949, Univ. California Publ. Ent., 8:221; Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:164,165,166; Linsley, MacSwain, and Smith, 1955, Pan-Pacific Ent., 31:175.

*Andrena (Onagrarendra) anograe knowltoni* Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:126-127; Linsley, MacSwain, and Raven, 1963, Univ. California Publ. Ent., 33:30, 39. **New synonymy.**

*Andrena (Onagrarendra) anograe*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:112; Tepedino, 1982, The Southwest Ent., 7:17.

*Andrena micranthophila* Cockerell, 1906, Bul. American Mus. Nat. Hist., 22:432; Frison, 1927, Bul. Illinois St. Nat. Hist. Surv., 16:231 (type list).

*Andrena (Melandrena) micranthophila*: Lanham, 1949, Univ. California Publ. Ent., 8:221; Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:166 synonymy).

*Andrena anograe* is one of only two species with females having largely black vestiture except pale on the thoracic dorsum and can be readily recognized by this character. The males of *anograe* are similar to those of *A. oenotherae* but have the propodeum outside of the dorsal enclosure and the lower lateral mesepisternal areas more finely sculptured.

**FEMALE: Measurements and Ratios.** N = 20; length, 12-15 mm; width, 3-4 mm; WL, M = 4.38±0.284 mm; FL/FW, M = 1.06±0.007; FOVL/FOVW, M = 2.88±0.053.

**Diagnosis.** Vestiture black except thoracic dorsum with hairs ochraceous to fox-red with few black hairs intermixed; vertex usually with some pale hairs, wing membranes hyaline, veins dark reddish brown to black; metasomal terga black without violaceous reflections. Galeae moderately long, dulled by fine dense shagreening; labral process slightly longer than half length of labrum, apex broad, thickened, usually bidentate, lateral margins concave. Clypeus with small, round, dense punctures, surface shiny, usually without median impunctate line; vertex above lateral ocellus equals one ocellar diameter or slightly less. Pronotum without humeral angle or vertical ridge laterally. Mesoscutum punctate, interpunctural surfaces dulled by fine shagreening. Scutellum with anterior punctate area moderately shiny. Propodeum with dorsal surface; enclosure (Fig. 7) coarsely rugulate, rugulae mostly transverse apically, irregular basally; dorsal surface outside of enclosure moderately punctatorugose; surfaces finely tessellate or shagreened. Mesepisternum with lower surface punctate, interpunctural spaces tessellate. Metasomal terga 2–4 with apical areas punctate in basal three-fifths or more, punctures separated mostly by 1 to 2 puncture

widths, basal area punctures separated largely by 1 to 3 puncture widths, surfaces shiny. Thoracic dorsum with hairs moderately long, longer than width of antennal scape; propodeum without corbicula laterally, hairs all long and plumose; scopal hairs long, simple, moderately abundant.

**MALE: Measurements and Ratios.** N = 20; length, 10–12 mm; width, 2.5–3.0 mm; WL, M =  $3.85 \pm 0.270$  mm; FL/FW, M =  $1.10 \pm 0.008$ ; FS1/FS2, M =  $1.41 \pm 0.034$ .

**Diagnosis.** Vestiture color as in female but mesepipleura occasionally with pale hairs intermixed with black and metasomal tergum 1 often with at least a few pale hairs basally; wing membranes hyaline, yellowish, veins red to reddish brown; metasomal terga black. Galeae as in female; labral process broad, strongly bidentate, reflexed; clypeus as in female; vertex above lateral ocellus equals about one ocellar diameter; flagellar segment 1 with minimum length equal to segment 3 and slightly longer than or equal to segment 2. Pronotum as in female; mesoscutum and scutellum posteriorly dulled, sculptured as in female but punctures slightly finer; mesepisternum (especially lower half) and propodeum outside of dorsal enclosure finely sculptured, with distinct punctures, not punctatorugose; dorsal enclosure reticulorugose (Fig. 12). Metasomal terga 2–5 with apical areas shiny, with small sparse punctures in basal half to two-thirds; basal areas slightly more coarsely punctate, shiny. Metasomal tergum 2 with basal area hairs long, at least half as long as those of tergum 1; hind tibiae with outer surface hairs long, sparse, almost as long along anterior margin as dorsal femoral hairs. Sternum 7 distinctly bidentate apically; sternum 8 not distinctly lobed apically but distinctly emarginate apically (Figs. 27 and 28).

**Type Material.** The holotype female of *Andrena anograe* Cockerell was taken at Colorado Springs, Colorado, middle of July, at flowers of white *Oenothera* (Ckll. No. 3,567) (USNM No. 5,808). The holotype female of *Andrena micranthophila* Cockerell was collected by W.P. Cockerell from east of Lake George, Park Co., Colorado, June 18, at flowers of *Chamaerhodos erecta* and is in the collection of the California Academy of Sciences (CAS No. 15,355). The holotype female of *Andrena knowltoni* was taken 5 miles S. of Green River, Emery Co., Utah, May 24, 1960, on *Stanleya pinnata* by G.F. Knowlton and is in the collection of the California Academy of Sciences (CAS No. 6,698).

**Distribution.** *Andrena anograe* is known to occur from central Wyoming, south to Colorado, and west to central Utah (Fig. 2). A single male labeled Tucson, Arizona, April 8, 1935, A.L. Melander in the INHS collection is here regarded as a mislabeled specimen. It may be one of the many specimens purchased by T.H. Frison and reputedly collected in Arizona by Oslar (Thorp, 1970). This species has been taken from May 5 through July 31, but chiefly in June and early July. A total of 96 females and 92 males were examined from the localities listed below (records from the literature are included).

COLORADO. CHAFFEE CO.: Mt. Princeton Hot Springs (1 mi. E.); Salida (1.5 mi. W). COSTILLO CO.: Sage Flats, Ute Creek. DENVER CO.: Denver. EL PASO CO.: Colorado Springs. GUNNISON CO.: Gunnison (7.6 and 8.4 mi. W). LARIMER CO.: Mishawauka. MONTROSE CO.: Cimarron (1.2 mi. W). PARK CO.: Lake George (E of); Wilkerson Pass. TELLER CO.: Florissant. NEW MEXICO. SAN JUAN CO.: Waterflow (2.5 mi. N). UTAH. EMERY CO.: Green River (2.5 mi. W, 6, 7 and 10 mi. N and 5 mi. S); Red Plateau (E foot); Woodside, (4.5 mi. N). GARFIELD CO.: Boulder. GRAND CO.: Crescent Junction; Johnson; Thompson. SAN JUAN CO.: Monticello. WYOMING. ALBANY CO.: Laramie (S. of). LARAMIE CO.: Cheyenne. SWEETWATER CO.

**Floral Records.** *Andrena anograe*, as its name suggests, collects pollen exclusively from species of Onagraceae, including the genus *Oenothera* subgenera *Anogra* and *Pachylophs*. It has been collected from flowers of the following plants.

*Chamaerhodos erecta*, *Cryptantha* sp., *Gaura* sp., *G. coccinea*, *Geranium fremontii*, *Oenothera* sp., *O. albicaulis*, *O. caespitosa*, *O. c.* var. *montana*, *O. coronopifolia*, *O. pallida trichocalyx*, *O. s. scapoidea*, *Oxytropis deflexa* var. *sericea*, *Penstemon* sp., *Senecio* sp., *Stanleya pinnata*.

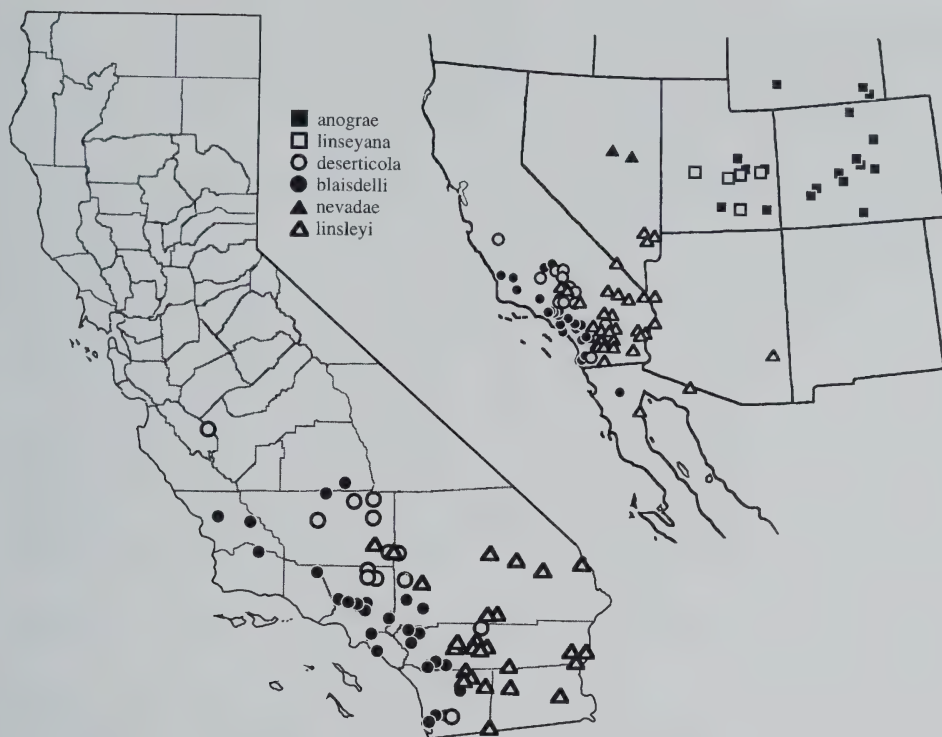


Fig. 2. Maps showing the known distributions of *A. anograe*, *A. linsleyana*, *A. deserticola*, *A. blaisdelli*, *A. nevadae*, and *A. linsleyi*. A separate map of the state of California is included to clarify location of localities.

### *Andrena* (*Onagrandra*) *linsleyana* Thorp

*Andrena* (*Onagrandra*) *linsleyana* Thorp, 1987, Pan-Pacific Ent., 63:194-198.

*Andrena linsleyana* is a large species related to *Andrena anograe*. The female of *linsleyana* is like the black specimens of *anograe* from Utah but has the ocelli enlarged and the scutellum entirely dull. The male of *linsleyana* has the vestiture entirely black, as does the male of *Andrena chylismiae*, but can be recognized by the slightly enlarged ocelli, the more finely sculptured propodeum outside of the enclosure, and the more densely punctate metasomal terga.

**FEMALE: Measurements and Ratios.** N = 5; length, 14–15 mm; width about 4.5 mm; WL, M =  $4.99 \pm 0.322$  mm; FL/FW, M =  $1.10 \pm 0.002$ ; FOVL/FOVW, M =  $2.97 \pm 0.149$ .

**Diagnosis.** Vestiture entirely black; wing membranes hyaline, slightly infumate, yellowish, veins dark reddish-brown to black; metasomal terga black without metallic reflections. Galeae as in *anograe*; labral process subtriangular or with thick apical part and concave sides (as in *anograe*), in two specimens with three angles apically, shiny. Clypeus with distinct, round, dense punctures, surface shiny, usually without complete median impunctate line or thin, if present; vertex above lateral ocellus equals distinctly less than one ocellar diameter, ocelli distinctly enlarged. Pronotum as in *anograe*. Mesoscutum sculptured as in *anograe*; scutellum densely punctate as in *anograe* and dulled by shagreening (not shiny in anterior fourth). Propodeum distinctly sculptured, as in *anograe*; mesepisterna with distinct punctures (not punctatorugose) and dulled by fine dense shagreening. Metasomal terga 2–4 densely punctate basally, punctures separated by half to one puncture width; apical areas punctate except narrow apical rim, surfaces shiny. Thoracic dorsum



with hairs long to moderately long, much longer than width of flagellum; propodeum without developed corbicula laterally, hairs long and plumose, grading from short below to longest dorsally; scopal hairs long, simple, moderately abundant.

**MALE: Measurement and Ratios.** N = 18; length, 11–13 mm; width, 2.5–3.5 mm; WL, M =  $4.30 \pm 0.340$  mm; FL/FW, M =  $1.16 \pm 0.016$ ; FS1/FS2, M =  $1.16 \pm 0.019$

**Diagnosis.** Vestiture entirely black as in female. Wing membranes hyaline, slightly infumate, veins reddish brown to dark brown; metasomal terga black, without metallic reflections. Galeae as in female; labral process broad, reflexed, bidentate. Clypeus as in female but without median line in any specimens; vertex above lateral ocellus equals slightly less than one ocellar diameter, ocelli enlarged; flagellar segment 1 longer than segment 2 and longer or equal to segment 3. Pronotum and mesoscutum as in *anograe* female. Scutellum as in female but usually shiny along anterior margin (basal fourth or less); propodeum and mesepisterna sculptured as in *anograe* male. Metasomal terga 2–5 sculptured as in female terga 2–4 but punctures slightly sparser. Metasomal tergum 2 with basal area hairs moderately long, almost half as long as those of tergum 1; hind tibiae with outer surface hairs long, sparse, along anterior margin almost as long as dorsal femoral hairs. Genital capsule illustrated by Thorp (1987, p. 197). Sternum 7 flattened apically with minute medial indentation, hairs sparse; sternum 8 as in *anograe* but without apical emargination (Figs. 29 and 30).

**Type Material.** The holotype female (USNM) of *linsleyana* was collected at Bullfrog Campground, Kane County (about 72 mi S of Hanksville, Wayne Co.), Utah, April 21, 1983 by F.D. and J.H. Parker.

**Distribution.** *Andrena linsleyana* is known only from Utah (Fig. 2). Males and females were collected on April 21 with females flying through July 10. A total of 27 females and 58 males were examined from the localities listed below.

UTAH: EMERY CO.: Gilson Butte (4 airline miles N); Wildhorse Creek N of Goblin Valley. GRAND CO.: Cisco; Elgin (E of). KANE CO.: Bullfrog Campground at Lake Powell (ca. 72 mi. S of Hanksville, Wayne Co.); Green River (7 mi. S). MILLARD Co.: Hatton.

**Floral Records.** *Andrena linsleyana* has been collected from *Oenothera pallida*, *Hymenopappus filifolius*, and *Stanleya pinnata* and is presumably an oligolege of flowers of the genus *Oenothera*.

**Remarks.** Thorp (1987) placed this species in a species complex including *Andrena chylismiae*, *nevadae*, *thorpi*, and *stagei*. However, we now consider this bee to be related to *Andrena anograe*, as evidenced by the sculpturing of the dorsum of the thorax, the mesepisterna, and the propodeum, as well as the shape of the labral process. It resembles *chylismiae* and keys out with it in our key because of the entirely black male vestiture.

### *Andrena (Onagrاندrena) omninigra* Viereck

*Andrena omninigra* Viereck, 1917, Trans. American Ent. Soc., 43:385–386; Linsley, 1938, Proc. California Acad. Sci., Ser. 4, 23:265, 277.

*Andrena grundeli* Linsley, 1938, Proc. California Acad. Sci., Ser. 4, 23:265, 267, 274–275.

*Andrena (Melandrena) grundeli grundeli*: Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:164, 165; Linsley, MacSwain and Smith, 1955, Pan-Pacific Ent., 31:176; Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:166; Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:127 (synonymy).

*Andrena (Melandrena) omninigra*: Lanham, 1949, Univ. California Publ. Ent., 8:221.

*Andrena (Onagrاندrena) omninigra*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:112, Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:127, 128 (synonymy); Linsley, 1972, Pan-Pacific Ent., 48:94–96; MacSwain, Raven and Thorp. 1973, Univ.

California Publ. Ent., 70:14, 41, 43, Tables 1, 2, 5–11. 13. 18. (synonymy).  
*Andrena* (*Onagrandrena*) *omninigra clarkiae* Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:127–128; MacSwain, Raven and Thorp, 1973, Univ. California Publ. Ent., 70:15–16. **New synonymy.**

*Andrena omninigra* females are distinctive in the extremely short dorsal thoracic vestiture and the deeply infumate, blackened wing membranes. The male of *omninigra* can be recognized by having black or dark brown hairs mixed with the pale on the thoracic dorsum and by having a tall vertex (above lateral ocellus vertex equals more than one ocellar diameter).

**FEMALE: Measurements and Ratios.** N = 20; length, 11–13 mm; width, 3–4 mm; WL, M =  $4.45 \pm 0.496$  mm; FL/FW, M =  $1.07 \pm 0.009$ ; FOVL/FOVW, M =  $3.15 \pm 0.058$ .

**Diagnosis.** Vestiture black; wing membranes deeply infumate, dark brown, veins black; metasomal terga black without violaceous reflections. Galeae moderately long, moderately shiny, dulled by fine shagreening. Labral process longer than half length of labrum, narrowed apically, lateral edges strongly concave, apical part narrower than scape base. Clypeus with round punctures crowded except in narrow medial impunctate line, surface shiny; vertex above lateral ocellus equals slightly more than one ocellar diameter. Pronotum without humeral angle or vertical ridge. Mesoscutum and scutellum punctate, punctures crowded, interpunctural surfaces moderately dulled by fine shagreening. Propodeum with distinct dorsal surface; dorsal enclosure coarsely rugulate, rugulae mostly longitudinal except irregular basally; surface outside of enclosure punctatorugose, surfaces shagreened or finely tessellate. Mesepisternum distinctly punctate, interpunctural spaces moderately shiny, shagreened. Metasomal terga with abundant round punctures separated mostly by half to one puncture width or slightly more, apices of terga narrowly impunctate; surfaces shiny, unshagreened. Thoracic dorsum with hairs extremely short, almost scalelike, shorter than width of antennal scape; propodeum with lateral surface with abundant, moderately short, simple, erect hairs, dorsal margin with moderately long plumose hairs no longer than twice length of internal hairs and often less; scopal hairs long, simple, moderately abundant.

**MALE: Measurements and Ratios.** N = 20; length, 9–12 mm; width, 2–3 mm; WL, M =  $3.92 \pm 0.385$  mm; FL/FW, M =  $1.11 \pm 0.008$ ; FS1/FS2, M =  $1.44 \pm 0.026$ .

**Diagnosis.** Vestiture color black except as follows: head with vestiture white except face above antennal fossae, along inner margins eyes, at least upper three-fourths of genal area with black hairs or white and black mixed. Thoracic hairs white to pale ochraceous except as follows: pronotum with some dark hairs especially above; mesoscutum with large patch of dark hairs or mixed white and black; scutellum usually with small medial patch of dark hairs or mixed; mesepipleuron and propodeum usually with black hairs mixed with white; tegulae with dark hairs. Tergal hairs black except basally on tergum 1 to 4 white (often terga 2, 3, and 4 with various amounts of black or brown and white hairs mixed), terga 5, 6, and 7 entirely black; sternal hairs from mostly white to mostly black; leg hairs on tibiae and tarsae black, basal segments black or mixed white and black. Wings distinctly infumate, but less than in female. Metasomal terga with coarse, round punctures separated mostly by one to two puncture widths; apical rims narrowly impunctate; surfaces unshagreened, shiny. Galeae as in female; labral process strongly reflexed, deeply emarginate apically, broad; clypeus as in female but usually without median impunctate line; vertex above lateral ocellus equals distinctly more than one ocellar diameter; flagellar segment 1 distinctly longer than segment 2, antennae relatively short. Pronotum as in female; mesoscutum as in female but punctures finer; propodeum sculptured as in female but dorsal enclosure with rugulae slightly finer. Metasomal terga 2–5 with apical areas shiny, with deep round punctures in basal three-fifths to two-thirds; basal areas slightly more sparsely punctate, shiny. Metasomal tergum 2 with basal area hairs at least half as long as those of



tergum 1. Hind tibiae with outer surface hairs moderately long, distinctly shorter than dorsal femoral hairs. Sternum 7 as in *linsleyana* but hairs abundant, short; sternum 8 distinctly capitate apically, not at all emarginate (Figs. 23 and 24).

**Type Material.** The holotype female of *A. (O.) omninigra* (CAS No. 4,046) was collected in California by E. Norton. The holotype female of *A. (O.) grundeli* (CAS No. 4,233) was collected from Nippinawasse (near Midway), Madera Co., California, May 22, 1931, by E.S. Ross. The holotype female of *A. (O.) clarkiae* (CAS No. 6,706) was collected from Arroyo Seco, Monterey Co., California, May 21, 1955, by P. Torchio.

**Distribution.** *Andrena omninigra* is known (Fig. 3) only from California (MacSwain, Raven, and Thorp, 1993, p. 13). The flight period for *omninigra* is late May to early July, males primarily in May, females primarily in early June. One record of a female in early March may be in error. A total of 293 females and 123 males were examined from localities listed below.

CALIFORNIA. BUTTE CO.: Arch Rock Tunnel (Highway 70, Feather River Canyon); Highway 70 (5 mi. W Butte-Plumas county line). CALAVERAS CO.: Mokelumne Hill; Railroad Flat (1.5 mi. E and 4 mi. S). CONTRA COSTA CO.: Antioch. EL DORADO CO.: Camino; Pollock Pines; Riverton; Snowline Camp. FRESNO CO.: Bass Lake (and 2 mi. E.); Kings Canyon (Ten-mile Creek); Sequoia National Forest (T13S, R26E, 7.8 mi. N Highway 180); Tollhouse (1.5 mi. W). KERN CO.: Bodfish (2 mi. S); Glenville (6.2 mi. E). LOS ANGELES CO.: Angeles Canyon; San Antonio Canyon. MADERA CO.: Nippinawasse (near Midway); North Fork (2.7 and 4.8 mi. N); Oakhurst. MARIPOSA CO.: El Portal; Mariposa (and 6 mi. S); Mormon Bar (2.8 mi. S and 6.5 mi. SW); Wawona; Yosemite Valley. MONTEREY CO.: Arroyo Seco; Arroyo Seco Camp. PLUMAS CO.: Elephant Butte (1 mi. N); Elephant Butte Tunnel (2.3 mi. E); Rock Creek (Jct. Highway 70, Feather River Canyon). SACRAMENTO CO.: Folsom. SAN BENITO CO.: Hollister. SAN DIEGO CO.: Mt. Laguna. SAN LUIS OBSIPO CO.: Santa Margarita (5 mi. NE). SANTA CRUZ CO.: Felton. SOLANO/YOLO CO.: Putah Canyon. TULARE CO.: California Hot Springs; Kaweah; Pine Flat (3.7 mi. SE); Sequoia National Park. TUOLUMNE CO.: 3,500 feet alt.; Buck Meadows-Mather; Strawberry; Twain Harte (4 mi. W).

**Biology.** Linsley (1972) records robber flies, *Callinicus calcanicus* (Loew), as predators on *A. omninigra* in early June 1970 near Railroad Flat, Calaveras County, California, while female bees were nectaring at flowers of mountain misery, *Chaemaebatia foliolosa* Benth. Although *A. omninigra* is an oligolege of *Clarkia*, none of its pollen host plants were in bloom in the vicinity. Linsley suggests that the bees were foraging in the shade to minimize absorption of radiant heat through their black integument. He further suggests that the flies developed an early search image for these black bees foraging in patches of flowers in the shade and continued to prey on them while ignoring other brightly colored *Osmia* and other *Andrena* species foraging in sunny patches of the flowers.

**Floral Records.** *Andrena omninigra* is an oligolege of *Clarkia* spp. (MacSwain, *et al.* 1973). It has been collected from flowers of the plants listed below.

*Brassica* sp., *Calochortus venustus*, *Cercocarpus betuloides* (as *douglasii*), *Chamaebatia foliolosa*, *Clarkia* sp., *C. amoena huntiana*, *C. biloba*, *C. cylindrica*, *C. dudleyana*, *C. mildrediae*, *C. purpurea*, *C. quadravulnera*, *C. rhomboidea*, *C. speciosa*, *C. s. polyantha*, *C. unguiculata*, *C. williamsoni*, *C. xantiana*, *Cryptantha* sp., *C. flaccida*, *Eriodictyon californicum*, *Eriogonum* sp., *Gilia capitata*, *Rhamnus californica*, *Sidalcea malvaeflora*.

### *Andrena (Onagrnadrena) bernardina* Linsley

*Andrena bernardina* Linsley, 1938, Proc. California Acad. Sci., Ser. 4, 23:265, 267, 275-276.



*Andrena* (*Melandrena*) *bernardina*: Lanham, 1949, Univ. California Publ. Ent., 8:221.

*Andrena* (*Melandrena*) *grundeli bernardina*: Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:164, 165, 166–167; Linsley, MacSwain and Smith, 1955, Pan-Pacific Ent., 31:176.

*Andrena* (*Onagrarendra*) *bernardina*: Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:128; MacSwain, Raven and Thorp, 1973, Univ. California Publ. Ent., 70:13, 16, 67.

*Andrena bernardina* Linsley is a small species from southern California that is similar and related to *Andrena omninigra* Provancher. The female of *bernardina* is like that of *omninigra* in having short hairs on the thoracic dorsum and very much blackened, deeply infumate wing membranes. This female, however, has the dorsal thoracic hairs somewhat longer than in *omninigra*, being about as long as the flagellar width. In addition the female of *bernardina* has the vertex above the lateral ocellus equal to about one ocellar diameter. The male of *bernardina*, like that of *omninigra*, has black hairs mixed with the pale on the mesoscutum and the scutellum, but has the vertex above the lateral ocellus equals no more than one ocellar diameter.

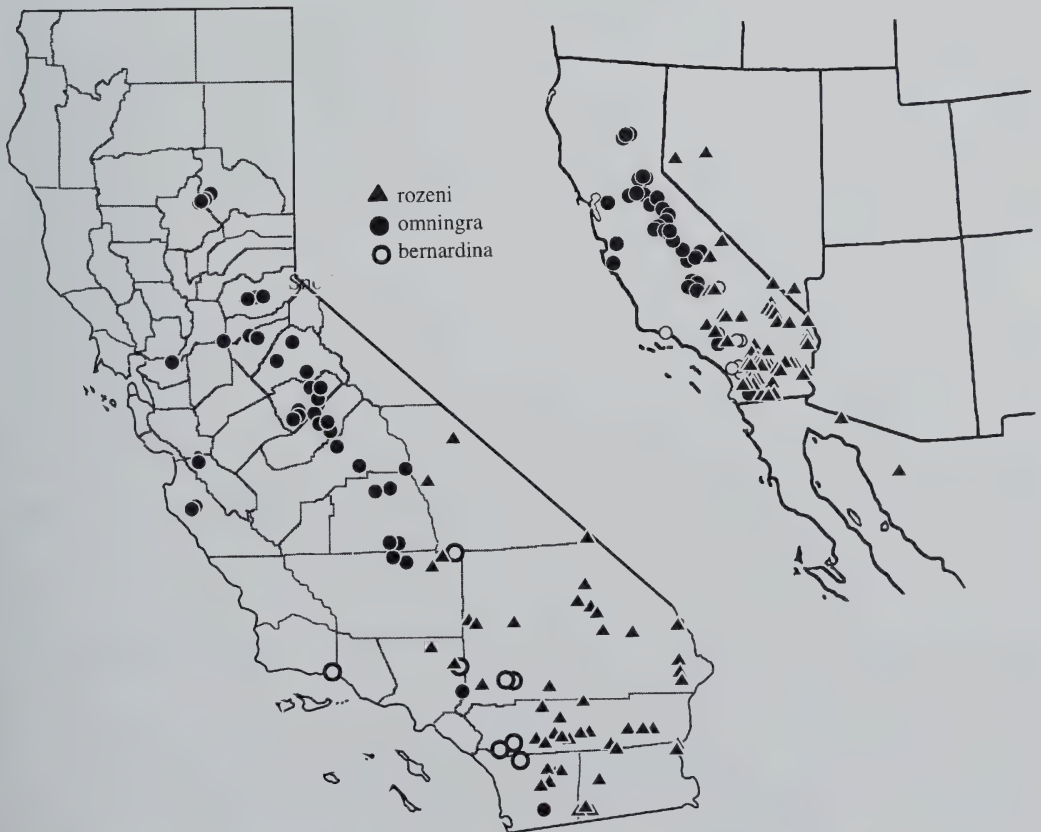


Fig. 3. Maps showing the known distributions of *A. rozeni*, *A. omninigra*, and *A. bernardina*.

**FEMALE: Measurements and Ratios.** N = 9; length, 11–12 mm; width, 3.0–3.5 mm; WL,  $4.09 \pm 0.232$  mm; FL/FW,  $1.02 \pm 0.004$ ; FOVL/FOVW,  $2.84 \pm 0.049$ .

**Diagnosis.** Vestiture black; wing membranes deeply infumate, dark brown, veins black; metasomal terga black without violaceous reflections. Galeae narrow, moderately shiny basally. Labral process as in *omninigra* but apical part broader, about as broad as base of scape or slightly broader. Clypeus as in *omninigra*; vertex above lateral ocellus equals about one ocellar diameter. Pronotum as in *omninigra*. Mesoscutum, scutellum and propodeum sculptured as in *omninigra*. Mesepisternum sculptured as in *omninigra* but punctures separated by half a puncture width or less. Metasomal terga with coarse round punctures separated mostly by half to two puncture widths, apical margins narrowly impunctate; surfaces shiny, shagreening extremely weak if present. Thoracic dorsum with hairs short but longer than in *omninigra*, at most as long as width of flagellum, somewhat irregular; propodeum with weakly developed corbicula laterally, inner surface with short, relatively simple hairs, anterior margin without long hairs, dorsal margin with long plumose hairs but these sparse; scopal hairs long simple, sparse, not hiding surface of tibia.

**MALE: Measurements and Ratios.** N = 4; length, 9–11 mm; width, 2.5–3.0 mm; WL, M =  $3.36 \pm 0.317$  mm; FL/FW, M =  $1.05 \pm 0.013$ ; FSI/FS2, M =  $1.16 \pm 0.085$ .

**Diagnosis.** Vestiture black except mesoscutum, scutellum and metanotum with hairs largely pale, white to grayish, with long black hairs intermixed posteromedially on mesoscutum and medially on scutellum. Wings hyaline, only slightly infumate. Galeae as in female; labral process strongly reflexed, emarginate apically, broad; clypeus shiny with crowded punctures, median impunctate line absent or incomplete and extremely narrow; flagellar segment 1 longer than either segment 2 or 3, segment 2 about equal to 3 or slightly shorter, antennae short; vertex as in female. Pronotum as in *omninigra*; mesoscutum, scutellum and propodeum sculptured as in *omninigra*. Metasomal terga 2–5 with apical and basal areas shiny, unshagreened, densely punctate with punctures separated largely by half to one or two puncture widths. Metasomal tergum with basal area hairs short; hind tibial hairs relatively short, about as long as greatest width of tibia or shorter. Sternum 7 with small, distinct, apical toothlike lobes with v-shaped median emargination, each lobe with several hairs; sternum 8 with apex distinctly broadened but not capitate, barely or not at all emarginate apicomediaally (Figs. 33 and 34).

**Remarks.** A male from Boron, Kern County, California, is probably *A. bernardina* although it is considerably paler than most males of this species. It has intermixed dark hairs on the mesosoma, lacks the white hairs on metasomal terga 1 and 2, and the propodeal enclosure is not as rugose. We think that this male is probably correctly placed under *bernardina*, but should be considered only as a questionable record.

**Type Material.** The holotype female of *A. (O.) bernardina* (CAS No. 4,542) was collected in Tetley Park, San Bernardino Mts., California, May 23, 1936, at flowers of *Potentilla glandulosa* by E.G. Linsley.

**Distribution.** *Andrena bernardina* is known to occur only in southern California (Fig. 3). It has been collected from mid-May until early July. In addition to the type material 19 female and 8 male specimens from localities listed below were examined.

CALIFORNIA. KERN CO.: Sand Canyon (3 mi W of Brown). Los Angeles Co.: San Antonio Canyon; Tanbark Flat. RIVERSIDE CO.: Sage (5 mi S); Temecula (9 mi E). SAN BERNARDINO CO.: Seeley Flat and Tetley Park, San Bernardino Mts. SAN DIEGO CO.: Mt. Palomar. SANTA BARBARA CO.: Carpenteria.

**Floral Records.** *Andrena bernardina* has been collected only from flowers of the plants listed below. It is presumably an oligolege of *Clarkia*, based on pollen from specimens reported by MacSwain et al. (1973). However, too few records exist to be able to designate whether this is, indeed, an oligolege or not. It has been taken from flowers of the plants listed below.

*Baccharis* sp., *Cryptantha* sp., *C. intermedia*, *Potentilla glandulosa*.

*Andrena (Onagrandrena) flandersi* Timberlake

*Andrena flandersi* Timberlake, 1937, Pan-Pacific Ent., 13:72; Cockerell, 1937, American Mus. Nov. No. 948, p. 14; Linsley, 1938, Proc. California Acad. Sci., Ser. 4, 23:266; 278.

*Andrena (Melandrena) flandersi*, Lanham, 1949, Univ. California Publ. Ent., 8:221; Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:164, 166, 167; Linsley, MacSwain and Smith, 1955, Pan-Pacific Ent., 31:176, 183.

*Andrena (Onagrandrena) flandersi*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:111, 113, 118–120; Linsley, MacSwain, and Raven, 1964, Univ. California Publ. Ent., 33:63, 64, 65, 72, 79, 80, 82, 88, 90, 91.

This moderate-sized, dark species from southern California can be recognized in the female sex by the short plumose hairs of the thoracic dorsum and the impunctate tergal apical areas. The male of *flandersi* also has the tergal apical areas impunctate.

**FEMALE: Measurements and Ratios.** N = 20; length, 10–11 mm; width, 3.0–3.5 mm; WL, M =  $3.42 \pm 0.102$  mm; FL/FW, M =  $1.06 \pm 0.006$ ; FOVL/FOVW, M =  $3.09 \pm 0.037$ .

**Diagnosis.** Vestiture black; wing membranes hyaline, scarcely or not infumate, veins dark brown; metasomal terga black without violaceous reflections. Galeae long, moderately dulled by fine shagreening. Labral process as in *omninigra* but apical part thick, at least as thick as base of scape, emarginate apically. Clypeus sculptured as in *omninigra*; vertex above lateral ocellus equals about one ocellar diameter. Pronotum without humeral angles or lateral ridge. Mesoscutum and scutellum punctate, punctures large, deep, separated mostly by half a puncture width or less, interpunctural surface shiny, unshagreened or only delicately so; metanotum with dense, extremely fine punctures dulling surface. Propodeum sculptured as in *omninigra* but surface outside of dorsal enclosure finely punctatorugose. Mesepisterna with distinct punctures in lower half, interpunctural surface dulled by coarse shagreening. Metasomal terga 2–4 with apical areas impunctate, shiny. Thoracic dorsum with hairs short, about as long as width of scape or shorter, erect, plumose, not scalelike, velvetlike; propodeal corbícula with internal hairs short, simple; long dorsal hairs sparse, long hairs absent along anterior margin; scopal hairs simple, long, moderately abundant.

**MALE: Measurements and Ratios.** N = 20; length, 9–11 mm; width, 2–3 mm; WL, M =  $3.26 \pm 0.159$ ; FL/FW, M =  $1.11 \pm 0.007$ ; FS1/FS2, M =  $1.13 \pm 0.024$ .

**Diagnosis.** Vestiture white except as follows: metasomal terga 3–5 often with brown hairs mixed with pale hairs basally. Wing membranes hyaline, not at all infumate. Galeae as in female; labral process strongly reflexed, large, bidentate; clypeus as in female; vertex above lateral ocellus equals one ocellar diameter; flagellar segment 1 equal to or slightly longer than segment 2 and equal to segment 3, antennae relatively short. Pronotum as in female; mesoscutum and scutellum shiny as in female but punctures slightly sparser. Propodeum and mesepisterna sculptured much as in female but propodeal dorsal enclosure with rugulae denser and less coarse. Metasomal terga 2–5 with apical areas impunctate, shiny; basal areas shiny with sparse punctures (Fig. 8). Metasomal tergum 2 with basal area hairs less than half as long as those of tergum 1. Hind tibiae with outer surface hairs moderately long, with at least a few extremely long hairs along anterior margin. Sterna 7 and 8 (Figs. 35 and 36) much as in *anograe*.

**Type Material.** The holotype female (CAS No. 14,359) of *Andrena (A.) flandersi* was collected about 11 miles SW of Victorville, San Bernardino County, California, May 5, 1936, at flowers of *Ericameria cooperi* by E.G. Linsley and P.H. Timberlake.

**Distribution.** *Andrena flandersi* is known to occur only in southern California in the Mojave Desert (Fig. 4). It has been collected from March 19 through June 14 from locali-



ties listed below. In addition to the holotype a total of 215 females and 32 males were examined.

CALIFORNIA. KERN CO.: Boron; Dove Well (5 mi. NW); Freeman Jct.; Mojave; Red Rock Canyon; Salt Wells (7 mi. W); Sand Canyon (3 mi. W of Brown); Short Canyon (6 mi. NW of Inyokern); Walker Pass (and 3 mi. SE). LOS ANGELES CO.: Acton; Little Rock (and 1 mi. W); Pallett Creek; Palmdale; Pearblossom (4 mi. S); Squaw Canyon (7 mi. S). SAN BERNARDINO CO.: Adelanto (20 mi. N); Big Panoche Creek; Desert Spring (5 mi. W); Kramer Hills; Kramer Junction (and 3 mi. S); Landers; Lucerne Valley; Morongo Valley; Phelan (2 mi. S); Red Mountain; Victorville (11 mi. SW). SAN DIEGO CO.: Borrego Springs. VENTURA CO.: Saticoy.

**Floral Records.** Although *Andrena flandersi* has not been collected frequently on Onagraceae, it has been taken on *Camissonia* (as *Oenothera*) (Linsley, MacSwain, and Raven, 1964) and is presumably an oligolege of flowers of that genus. Most females examined by the authors have at least a few *Camissonia* pollen grains in their scopae. This species has been collected from flowers of the plants listed below.

*Baccharis* sp., *Camissonia campestris*, *C. claviformis claviformis*, *C. contorta*, *C. kernensis*, *Chaenactis* sp., *Coreopsis* sp., *C. bigelovii*, *C. californica*, *Cryptantha* sp., *Ericameria cooperi*, *Lasthenia californica*, *Layia* sp., *L. glandulosa*, *Malacothrix* sp., *Oenothera* (= *Camissonia* ?) sp., *Salix* sp.

### *Andrena (Onagrandrena) furva* Linsley and MacSwain

*Andrena (Onagrandrena) furva* Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:117–118; Linsley, MacSwain, and Raven, 1964, Univ. California Publ. Ent., 33:64, 73, 79; Linsley, MacSwain, Raven, and Thorp, 1973, Univ. California Publ. Ent., 71:26, 27, 32–33, 47, 51, 56; MacSwain, Raven and Thorp, 1973, Univ. California Publ. Ent., 70:46.

The female of *Andrena furva* is similar to that of *omninigra* and related species but has entirely black vestiture and short dorsal thoracic hairs. The male of *furva* was unknown and a complete description is supplied below. This male is one of those species with entirely white vestiture and has the galeae small and shiny as in *Andrena blaisdelli*, but differs from that species by the longer vertex, shorter first flagellar segment, and shorter, more distinct sternal fimbriae as described below.

**FEMALE: Measurements and Ratios.** N = 20; length, 10–11 mm; width, about 3 mm; WL, M =  $3.20 \pm 0.120$  mm; FL/FW, M =  $0.97 \pm 0.004$ ; FOVL/FOVW, M =  $3.01 \pm 0.044$ .

**Diagnosis.** Vestiture black; wing membranes hyaline, not infumate or only slightly so, veins dark brown; metasomal terga black without metallic reflections. Galeae short, narrow, shiny, slightly shagreened in apical halves or less or unshagreened. Labral process with apical part narrow, sides strongly concave, apex usually deeply emarginate; clypeus with round crowded punctures, without impunctate midline or this incomplete and narrow; vertex above lateral ocellus equals one ocellar diameter or rarely slightly more. Pronotum without dorsal angle or lateral ridge. Mesoscutum and scutellum with small dense punctures separated mostly by half a puncture width, interpunctural spaces dulled by fine shagreening (Fig. 9). Propodeum with distinct dorsal surface; dorsal enclosure coarsely, irregularly rugulate; surface outside of enclosure moderately coarsely punctatorugose. Mesepisterna coarsely punctatorugose. Metasomal terga 2 and 3 with basal areas with punctures round, deep, crowded, separated mostly by half a puncture width, slightly sparser near apical area, apical areas with apical half impunctate, basal half punctured similar to basal areas; surfaces shiny, unshagreened. Thoracic dorsum with hairs short, mosslike,

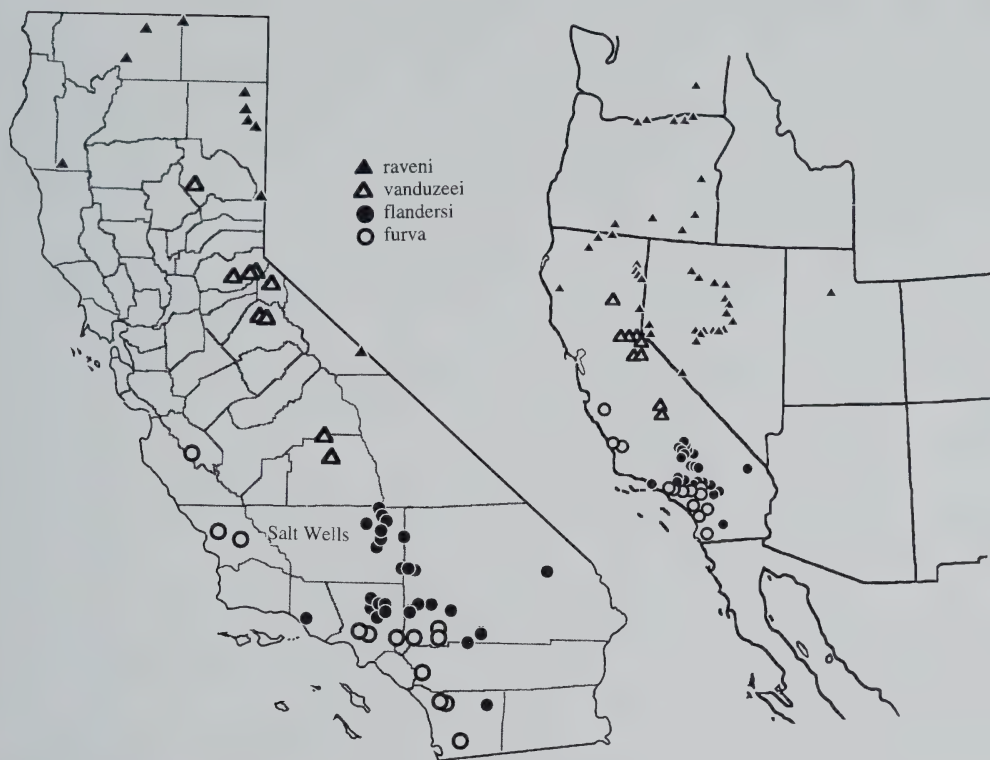


Fig. 4. Maps showing the known distributions of *A. flandersi*, *A. raveni*, *A. vanduzeei*, and *A. furva*.

shorter than width of antennal scape; propodeum with corbicula as in *flandersi*; scopal hairs simple, abundant.

**MALE: Measurements and Ratios.**  $N = 20$ ; length, 8–11 mm; width, 2.5–3.0 mm; WL,  $M = 3.17 \pm 0.172$  mm; FL/FW,  $M = 1.07 \pm 0.007$ ; FS1/FS2,  $M = 1.04 \pm 0.013$ .

**Integumental Color.** Black except as follows: mandible with apical fourth rufescent, terga with apical areas piceous, wing membranes hyaline, not or only slightly infumate.

**Structure.** Antennae relatively short, in repose not reaching scutellum; scape length equals first two and one-half flagellar segments; flagellar segment 1 about as long as segment 2 or slightly longer, usually shorter than segment 3; segments beyond 3 all slightly longer than broad. Eyes each almost three times as long as broad, inner margins diverging towards vertex. Mandibles not decussate. Galeae as in female. Maxillary palpus short, with segmental ratio about as 1.0:1.0:0.8:0.8:0.6:0.8. Labial palpus with ratio about as 1.0:0.3:0.3:0.5. Labral process large, deeply emarginate, strongly reflexed; labrum apical to process without sulcus or cristae. Clypeus moderately long, median length equals about half or slightly less of interocular width; densely punctate, interpunctural surfaces shiny, without median impunctate line. Supraclypeal area dulled by minute punctures and shagreening. Face above antennal fossae with longitudinal rugulae, diverging medially towards ocelli; vertex above lateral ocellus equals slightly more than one ocellar diameter, never less than one. Genal area slightly broader than eye in profile. shiny, punctate except in narrow zone near eye margin.

Pronotum without humeral angles or lateral ridge. Mesoscutum and scutellum with crowded punctures, surface dulled by shagreening except scutellum occasionally moderately shiny. Propodeum sculptured as in female but dorsal enclosure with rugulae fine; mesepisterna punctatorugose as in female.

Metasomal terga 2–5 with basal areas punctate, punctures separated by half to one or two puncture widths, surfaces shiny, shagreening slight, if present; apical areas with punctures at least in basal halves, shiny. Tergum 7 with distinct, narrow, triangular pseudopygidial areas, lateral edges often turned slightly up. Sterna 2–5 with basal areas distinctly punctate, punctures separated mostly by 2 to 3 puncture widths, surfaces moderately shiny; apical areas impunctate. Sternum 7 with apical lobe elongate, weakly emarginate, with sparse, fine hairs; Sternum 8 strongly capitate apically, neck region with abundant hairs but not covering apical margin (Figs. 37 and 38).

**Vestiture.** White except vertex occasionally with a few yellowish brown hairs and hind basitarsi with inner surfaces with pale yellow hairs. Clypeus with dense beard; hind basitarsus with hairs along anterior margin moderately long; sterna 2–5 with dense subapical fimbriae of relatively short hairs.

**Type Material.** The holotype female of *Andrena (O.) furva* (CAL No. 6,703) was collected 4.5 miles NE of Santa Margarita, San Luis Obispo County, California, April 28, 1959, by J. W. MacSwain.

**Distribution.** This species is known only from southern California (Linsley, MacSwain, Raven, and Thorp, 1973, p. 33) (Fig. 4). It has been collected from April 14 through May 1. In addition to the holotype, a total of 22 females and 23 males were examined from localities listed below.

CALIFORNIA. LOS ANGELES CO.: Altadena; Claremont; La Crescenta. RIVERSIDE CO.: Elsinore (4 mi. E in Railroad Canyon). SAN BENITO CO.: Pinnacles Nat. Monument. SAN BERNARDINO CO Co.: Deep Creek; Fontana (4 mi. N). SAN DIEGO CO.: Descanso-Alpine transect; Frey Creek, Pauma Valley. SAN LUIS OBISPO CO.: La Panza Camp (12 mi. NE of Pozo); Santa Margarita (4.5 mi. N and 5 mi. NE).

**Floral Records.** *Andrena furva* has been collected from flowers of the following plants. *Camissonia campestris*, *C. contorta*, *Clarkia cylindrica*, *Cryptantha* sp. and *C. intermedia*.

### *Andrena (Onagrاندrena) oenotherae* Timberlake

*Andrena oenotherae*: Bohart, 1937, Pan-Pacific Ent., 13:54 (**Nomen nudum**).

*Andrena oenotherae* Timberlake, 1937, Pan-Pacific Ent., 13:6971; Linsley, 1938, Proc. California Acad. Sci., Ser. 4, 23:266, 267; Rust, Menke, and Miller, 1985, in Menke and Miller, Entomology of the California Channel Islands, San Diego, California, p. 42.

*Andrena (Melandrena) oenotherae*: Lanham, 1949, Univ. California Pub. Ent., 8:221; MacSwain and Smith, 1955, Pan-Pacific Ent., 31:173, 175, 176, 178, 180, 181–182, 183.

*Andrena (Onagrاندrena) oenotherae*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:111, 112–113, 116–118, 119, 120; Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:125, 128; Linsley and MacSwain, 1963, Pan-Pacific Ent., 39:189, 190, 192, 196; Linsley, MacSwain, Raven, and Thorp, 1973, Univ. California Publ. Ent., 71:33–34; Davis and LaBerge, 1975, Nat. Hist. Surv., Biol. Notes No. 95, p. 10.

*Andrena (Onagrاندrena) convallaria convallaria* Linsley and MacSwain, 1963, Pan-Pacific Ent., 39:190–193. **New synonymy.**

*Andrena (Onagrاندrena) convallaria subhyalina* Linsley and MacSwain, 1963, Pan-Pacific Ent., 39:193–194; Linsley, MacSwain, and Raven, 1963, Univ. California Pub. Ent., 33:71–72. **New synonymy.**

*Andrena (Onagrاندrena) oraria oraria* Linsley and MacSwain, 1963, Pan-Pacific Ent., 39:194–196; Linsley, MacSwain, Raven, and Thorp, 1973, Univ. California Publ. Ent., 71:34–35. **New synonymy.**



*Andrena (Onagrarendra) oraria actitis* Linsley and MacSwain, 1963, Pan-Pacific Ent., 39:196; Linsley, MacSwain, Raven, and Thorp, 1971, Univ. California Publ. Ent., 71:35. **New synonymy.**

*Andrena oenotherae* is one of our most common *Onagrarendra*. The female can be recognized by being entirely black with relatively long dorsal thoracic vestiture, relatively dense scopal hairs, and relatively densely punctate clypeus and metasomal terga. The male of *oenotherae* has the dorsal thoracic hairs white without black hairs, clypeal hairs all or mostly pale, and the mesepisternum and propodeal surface outside of the dorsal enclosure coarsely sculptured, punctatorugose.

**FEMALE: Measurements and Ratios.** N = 20; length, 11–14 mm; width, 3–4 mm; WL, M =  $3.90 \pm 0.196$  mm; FL/FW, M =  $1.06 \pm 0.010$ ; FOVL/FOVW, M =  $3.06 \pm 0.050$ .

**Diagnosis.** Vestiture black; wing membranes hyaline, slightly infumate, veins dark brown to black; metasomal terga black without metallic reflections. Galeae moderately long, dulled by fine shagreening; labral process (Fig. 11) longer than half length of labrum, sides strongly concave, apical part narrower than base of first flagellar segment, usually entire, rarely somewhat knobbed and slightly emarginate at apex (apex appears heart shaped). Clypeus with punctures large, deep, crowded, separated mostly by half a puncture diameter, larger apicomediaally, surface shiny, unshagreened except occasionally shagreened near base, without median impunctate line; vertex above lateral ocellus equals one ocellar diameter or slightly less; ocelli not enlarged or only slightly so. Pronotum without humeral angle or vertical ridge laterally. Mesoscutum with abundant small punctures separated mostly by half a puncture width, surface dulled by fine dense shagreening; scutellum punctatorugose, shagreened. Propodeum with distinct dorsal surface; dorsal enclosure with coarse irregular rugulae (Fig. 12), often with median longitudinal ruga; dorsal surface outside of enclosure and posterior surface moderately coarsely punctatorugose; surfaces moderately dulled by shagreening. Mesepisternum punctatorugose, dull. Terga 2–4 apical areas with punctures separated mostly by 1 to 3 puncture widths, basal areas with punctures separated mostly by half to one puncture widths, surfaces shiny. Thoracic dorsum with hairs much longer than width of scape; propodeum without distinct corbicula laterally, hairs long and plumose; scopal hairs long simple, moderately abundant, hiding surface to some degree.

**MALE: Measurements and Ratios.** N = 20; length, 9–11 mm; width, 2–3 mm; WL, M =  $3.49 \pm 0.201$  mm; FL/FW, M =  $1.07 \pm 0.005$ ; FS1/FS2, M =  $1.24 \pm 0.025$ .

**Diagnosis.** Vestiture black except as follows: mesonotum, scutellum and metanotum with dorsal surfaces with long white hairs; vertex with some long white hairs mixed with black; metasomal tergum 1 with pale hairs basally (may be mixed with long black hairs), tergum 2 occasionally with basal area with several pale hairs especially basomedially. Wing membranes hyaline, slightly infumate apically, veins dark reddish brown to black. Metasomal terga black, apical areas dark brown, slightly translucent. Galeae as in female; labral process bidentate; clypeus densely punctate, without median impunctate line; surface shiny, unshagreened; vertex above lateral ocellus equals about one ocellar diameter; flagellar segment 1 with minimum length equal to segment 3, usually slightly longer than segment 2. Pronotum as in female; mesoscutum and scutellum as in female but punctures smaller; propodeum as in female but dorsal enclosure with rugulae almost always irregular (Fig. 10), rarely with median ruga; mesepisterna punctatorugose, dull. Metasomal terga 2–5 with apical area punctures separated by one to three puncture widths, often restricted to basal half of apical area, surfaces shiny, lightly shagreened if at all. Metasomal tergum 2 with basal area hairs long, mediobasally half as long as those of tergum 1 or longer; hind tibiae with outer surface hairs long, sparse, along anterior margin some almost as long as dorsal femoral hairs. Genital capsule as in Figs. 13 and 14. Sternum 7 with apical margin in two rounded lobes and median emargination; sternum 8 weakly capitate, not at all or barely emarginate apicomediaally (Figs. 41 and 42).

**Type Material.** The holotype female of *Andrena (O.) oenotherae* (CAS No. 14368) was collected at Gavilan, Riverside County, California, March 20, 1932 by C.M. Dammers from flowers of *Oenothera* (perhaps *Camissonia*) sp. The holotype female (CAS No. 11,275) of *A. (O.) convallaria* was collected from 2.5 miles S of Livingston, Merced County, California, March 20, 1960 by G.I. Stage from flowers of *Camissonia* (as *Oenothera*) *campestris*. The holotype female of *A. (O.) subhyalina* (CAS No. 11,276) was collected at Boron, Kern County, California, April 3, 1959, by J.W. MacSwain from *Camissonia* (as *Oenothera*) *campestris*. The holotype female of *A. (O.) oraria* (CAS No. 11,278) was collected from beach one mile NE of Point Reyes light-house, Marin County, California, April 19, 1959, by J. W. MacSwain from flowers of *Camissonia* (as *Oenothera*) *cheiranthifolia cheiranthifolia*. The holotype female of *A. (O.) actitis* (CAS No. 11,279) was collected at Fleishhacker Zoo (SW corner of), San Francisco, California, May 21, 1959 by J.W. MacSwain from flowers of *Camissonia* (as *Oenothera*) *cheiranthifolia cheiranthifolia*.

**Distribution.** *Andrena oenotherae* is known to occur from central cismontane California south into Baja California del Norte (Linsley, MacSwain, Raven, and Thorp, 1973, p. 30) (Fig. 5). Timberlake (1937) lists this species from Arizona (Cave Creek, Chiricahua Mts.), but this has not been verified. It has been collected from January 16 through July 9 but mostly from March through early June. A total of 1,119 females and 499 males were examined from localities listed below.

CALIFORNIA. CONTRA COSTA CO.: Antioch. FRESNO CO.: Coalinga (5 mi. W); Jacolitos Canyon; Kerman (9 mi. W). IMPERIAL CO.: Coyote Wells (6 mi. W); Sunrise Butte. KERN CO.: Bakersfield (18 and 20 mi. E, 7.3 mi. N); Bealville; Blackwell's Corner (and 9.6 mi. N); Boron; Edison (5 and 6 mi. E); Frazier Park; Frazier River (6 air mi. E of Tupman); Lebec; Short Canyon (6.5 mi. NW Inyokern); Tejon Canyon; Weldon (and 10 mi. S). LOS ANGELES CO.: Alatimos Bay; Altadena; Azusa (3 mi. N); Camp Baldy; Claremont; Devil's Punchbowl; Elizabeth Lake Canyon; El Segundo Sand Dunes; Glendale; Irwindale; La Crescenta; Lancaster (and 18 mi. W); Little Rock; Manhattan Beach; Mescal Wildlife Sanctuary; Palmdale; Pasadena; Point Dume; Redondo Beach; San Gabriel Canyon; San Gabriel Mts.; San Gabriel Wash; Whittier. MADERA CO.: Oakhurst (Cemetery and 3.7 mi. W). MARIN CO.: Dillon Beach; Point Reyes Lighthouse (1 mi. NE); Point Reyes National Seashore (North Beach). MERCED CO.: Livingston (2 mi. SW and 2.5 mi. S). MONTEREY CO.: Bradley (1.5 mi. W). ORANGE CO.: Balboa Island; Laguna Beach; Newport; Newport (upper) Bay; Newport Beach. RIVERSIDE CO.: Elsinore (and 4 mi. E); Gavilan; Hemet (and 6 mi. S); Homeland; Palm Springs; Mira Loma; Perris; Riverside; Sage (5 mi. S); Santa Ana River; Soboda Hot Springs; Sunnymead; Temecula (7 and 9 mi. E); Wineville. SACRAMENTO CO.: Brannon Island State Park. SAN BERNARDINO CO.: Adelanto; Alta Loma; Desert Springs; Kramer Junction (4 mi. S); Phelan (2 mi. S); Redlands; San Bernardino (10 mi. W); Verdemon; Victorville (11 mi. S). SAN DIEGO CO.: Border Field State Beach; Borrego; Carlsbad (and 2 mi. S); Coastal Sage area; Coronado; Del Mar; Dulzura; Jacumba; Lakeside; Newton; Oceanside; Pauma; Pine Valley (1 mile N); San Diego and Mission Bay; San Pasqual (4 mi. E); Solana Beach. SAN FRANCISCO CO.: Fleishaker Zoo; Sand Dunes; San Francisco. SAN LUIS OBISPO COUNTY: Bee Rock (1.8 mi. W); Creston (2.5 mi. S); Santa Margarita (4.5 and 5 mi. NE); Shandon (6.8 mi SW); Simmler (10 mi. W). SANTA BARBARA CO.: Cuyama; Goleta; New Cuyama (and 28 mi. NW); Pine Canyon Guard Station (1.6 mi. W and 2.6 mi. E); Santa Cruz Island (Christy Beach and Fraser Point); Santa Rosa Island (Carrington Point and Skunk Point); Ventucopa (Santa Barbara Canyon). STANISLAUS CO.: Turlock. TULARE CO.: Fairview (1 mi. S); Johnsondale; Tipton (2.4 mi. S); Tulare (airpark and 4 mi. S). VENTURA CO.: Chuchupate Ranger Station (base of Frazier Mt.); Fillmore; Gorman (5 mi. S in Hungry Valley); Mugu Lagoon (Point Mugu); Point Mugu Naval Air Station (Area 1 and 2); Quatal Canyon (NW corner of county); San Buenaventura State Park (S end); Saticoy; Upper



Cuyama Canyon; Ventura. MEXICO. BAJA CALIFORNIA DEL NORTE: Descanso Bay; Ensenada (3 mi. S); La Zapopita, Valle de Trinidad; Santo Tomas (7 mi. N).

**Floral Records.** *Andrena oenotherae* is an oligoledge of matinal blooming flowers of the genus *Camissonia* (Linsley *et al.*, 1973) and has been collected from flowers of the plants listed below.

*Acacia greggii*, *Agoseris heterophylla*, *Allysum maritimum*, *Anisocoma acaulis*, *Brassica* sp., *Cakile edentulata*, *Calandrinia* sp., *Camissonia* sp., *C. bistorta*, *C. californica*, *C. campestris*, *C. c. obispoensis*, *C. cheiranthifolia cheiranthifolia*, *C. c. suffruticosa*, *C. claviformis claviformis*, *C. contorta*, *C. kernensis*, *C. micrantha*, *C. ovata*, *C. pallida*, *C. sierrae*, *Capsella bursa-pastori*, *Chaenactis* sp., *Chrysanthemum coronarium*, *Coreopsis* sp., *C. bigelovii*, *C. californica*, *Croton californicus*, *Cryptantha* sp., *C. clevelandii*, *C. intermedia*, *Encelia actoni*, *Ericameria* sp., *E. cooperi*, *Eriogonum fasciculatum*, *Erodium* sp., *Gilia* sp., *Hemizonia kelloggii*, *Isomeris arborea*, *Lantana* sp., *Lasthenia* sp., *Layia glandulosa*, *L. platyglossa*, *Lupinus* sp., *Malacothrix* sp., *Melilotus alba*, *Mirabilis californica*, *Oenothera* (= *Camissonia*) sp., *Phacelia* sp., *Potentilla* sp., *Rhaphanus sativus*, *Salix* sp., *S. laevigata*, *S. lasiolepis*, *Sisymbrium* sp., *Vicia americana*, *Viguiera* sp.

### *Andrena* (*Onagrandra*) *vespertina* Linsley and MacSwain

*Andrena* (*Onagrandra*) *vespertina* Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:123-125; Linsley and MacSwain, 1963, Pan-Pacific Ent., 39:193; Linsley, MacSwain, Raven and Thorp, 1973, Univ. California Publ. Ent., 71:27, 35-36, fig. 15, table 10.

*Andrena vespertina* is a large black bee active in the late afternoon and evening, as well as in the early morning. The female of *vespertina* is similar to that of *oenotherae* but has more densely punctate metasomal terga and the mesoscutal punctures are smaller and denser. The male of *vespertina* is like that of *boronensis* in having white clypeal hairs and white dorsal thoracic hairs without an intermixture of black hairs but has no white hairs on the pleural areas of the thorax and has the metasomal terga much more densely punctate.

**FEMALE: Measurements and Ratios.** N = 20; length, 13.0-13.5 mm; width, 3.0-3.5 mm; WL, M = 4.06±0.185 mm; FL/FW, M = 1.04±0.004; FOVL/FOVW, M = 2.82±0.037.

**Diagnosis.** Vestiture black; wing membranes moderately infumate, yellowish brown, veins dark brown to black; metasomal terga without metallic reflections. Galeae as in *oenotherae*; labral process with apical portion narrow as in *oenotherae*. Clypeus sculptured as in *oenotherae*. Vertex and ocellus as in *oenotherae*. Pronotum without humeral angle or lateral ridges (Fig. 15); mesoscutum and scutellum sculptured as in *oenotherae* but punctures slightly smaller and denser, separated entirely by half a puncture width or less, surface dull, shagreened; propodeum sculptured as in *oenothera*; mesepisternum finely punctatorugose, dull, shagreened. Metasomal terga 2 and 3 with apical area punctures separated mostly by 1 to 3 puncture widths, basal area (especially in median third) with punctures dense, separated mostly by half a puncture width or less, contrasting somewhat with slightly more sparsely punctate apical area; surfaces shiny. Thoracic dorsum with hairs long, dense; propodeum without distinct corbicula, hairs long and plumose; scopal hairs long, simple, moderately abundant, hiding surface to some degree.

**MALE: Measurements and Ratios.** N = 20; length, 11-12 mm; width, 2.5-3.0 mm; WL, M = 3.73±0.289 mm; FL/FW, M = 1.13±0.004; FS1/FS2, M = 1.19±0.015.

**Diagnosis.** Vestiture black except as follows: clypeal hairs entirely white, facial hairs white except along inner margins compound eyes, vertex with white hairs, thorax with dorsal hairs white, without dark hairs, pleural hairs black without white hairs in upper part, metasomal tergum 1 usually entirely or partly white. Wing membranes hyaline, slightly



infumate apically, veins dark brown to black; metasomal terga black, apical areas not or only slightly translucent. Galeae as in female; labral process and clypeal sculpturing as in *oenotherae*; vertex above lateral ocellus equals about one ocellar diameter; flagellar segments as in *oenotherae*. Pronotum as in *oenotherae* female; mesoscutum and scutellum sculptured as in *oenotherae* female but mesoscutal punctures slightly denser and pleural punctures distinct (not punctatorugose); propodeum with dorsal enclosure coarse, irregularly rugose; surface outside of enclosure, dull, finely sculptured, tessellate with indistinct punctures slightly roughening surface. Metasomal terga 2–5 (especially 2 and 3) with apical area punctures separated by 1 to 3 puncture widths, often restricted to basal half or slightly more; basal area punctures dense, separated mostly by half to one or two puncture widths and contrasting with more sparsely punctate apical areas. Metasomal tergal hairs and hind tibial hairs as in *oenotherae*. Sternum 7 with broad apical lobes and small apicomedian emargination, hairs weak but abundant; sternum 8 capitate with weak apicomedian emargination, hairs slender relatively sparse (Figs. 47–48).

**Type Material.** The holotype female of *Andrena (Onagrarendra) vespertina* (CAS No. 6,710) was collected 18 miles E of Bakersfield, Kern County, California, April 19, 1958, at flowers of *Camissonia boothii* (as *Oenothera decorticans*) by E.G. Linsley.

**Distribution.** *Andrena vespertina* is known from the type locality and Del Puerto Canyon, 21 mi. W Patterson, Stanislaus Co. (Fig. 5). It was collected several times from March 9 through June 12 (Linsley *et al.* 1973). We have examined 74 females and 95 males.

CALIFORNIA. KERN CO.: Bakersfield (18 mi. E). STANISLAUS CO.: Del Puerto Canyon (21 mi. W of Patterson).

**Floral Records.** *Andrena vespertina* is considered to be an oligolege of *Camissonia boothii* and is known to forage during late evenings. It has been collected from flowers of the plants listed below.

*Camissonia boothii* (as *decorticans*), *C. campestris*, *Isomeris arborea*.

### *Andrena (Onagrarendra) boronensis* Linsley and MacSwain

*Andrena (Onagrarendra) boronensis* Linsley and MacSwain, 1962, Pan-Pacific Ent..

38:49–51; Linsley, MacSwain, and Raven, 1963, Univ. California Pub. Ent., 33:69–71.

*Andrena (Onagrarendra) eulobi* Linsley and MacSwain, 1963, Pan-Pacific Ent.,

39:197; Linsley, MacSwain, Raven, and Thorp, 1973, Univ. California Publ.

Ent., 71:31–32. **New synonymy.**

*Andrena boronensis* is closely related to *A. oenotherae* from which it can be separated in both sexes by the more sparse metatergal punctation. In the female, terga 2 and 3 have the apical area punctures separated largely by three to five puncture widths and the punctures are minute in size.

**FEMALE: Measurements and Ratios.** N=20; length, 12–14 mm; width, 3–4 mm; WL, M =  $3.88 \pm 0.193$  mm; FL/FW, M =  $1.09 \pm 0.007$ ; FOVL/FOVW, M =  $3.15 \pm 0.058$ .

**Diagnosis.** Vestiture black; wing membranes hyaline, slightly infumate apically, veins dark brown to black; metasomal terga black without metallic reflections. Galeae as in *oenotherae*; labral process with narrowed apical portion occasionally narrow as in *oenotherae*, usually about as broad as base of scape or almost so, occasionally weakly emarginate apically. Clypeus sculptured as in *oenotherae*. Vertex and ocelli as in *oenotherae*. Pronotum without humeral angle or vertical ridge laterally; mesoscutum, scutellum, mesepisternum and propodeum sculptured as in *oenotherae*. Terga 2 and 3 with apical areas with punctures separated mostly by 3 to 5 puncture widths, punctures minute, basal areas with punctures separated by 1 to 3 or more puncture widths, sparse especially in median third, surfaces shiny. Thoracic dorsum with hairs long; propodeum without distinct corbicula laterally, hairs long and plumose; scopal hairs long, simple, moderately abundant, hiding surface to some degree.

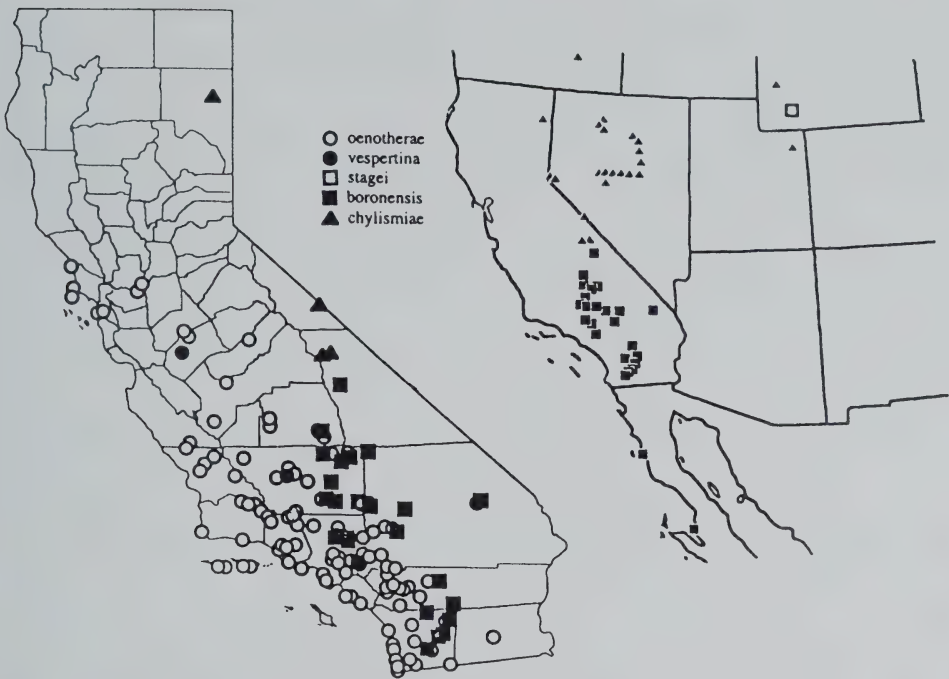


Fig. 5. Maps showing the known distributions of *A. oenotherae*, *A. vespertina*, *A. chylismiae*, *A. stagei*, and *A. boronensis*.

**MALE: Measurements and Ratios.**  $N = 20$ ; length, 9–10 mm; width, 2–3 mm; WL,  $M = 3.51 \pm 0.143$  mm; FL/FW,  $M = 1.14 \pm 0.009$ ; FS1/FS2,  $M = 1.25 \pm 0.019$ .

**Diagnosis.** Head with vestiture white except as follows: long black hairs mixed with white on vertex, on face along inner margins of compound eyes and occasionally mixed with black on face above clypeus, on labrum, and on genal area (some white usually present on lower genal area below level of mandible). Thorax white dorsally, usually including a few to many long white hairs on dorsal surface of propodeum; pleural hairs black with white at least dorsally near wings. Leg hairs black but some white hairs often present on femora. Metasomal hairs black with long white hairs dorsally on tergum 1 and a few mediobasally on tergum 2. Wing membranes hyaline, slightly infumate apically at most, veins dark reddish brown to black; metasomal terga black, without metallic reflections. Galeae as in female; labral process bidentate; clypeus densely, finely punctate, surface shiny; vertex above lateral ocellus equals about one ocellar diameter; flagellar segment 1 with minimum length usually slightly longer than segment 2, about equal to segment 3. Pronotum and thoracic sculpturing, including propodeum, as in *oenotherae* female. Metasomal terga sculptured much as in female but punctures usually sparser; tergum 2 with basal area hairs and tibial hairs as in *oenotherae*. Sternum 7 with apical teeth small, crowded together, median emargination weak with fine hairs; sternum 8 much as in *oenotherae* but apical hairy lobe somewhat narrower (Figs. 43 and 44).

**Type Material.** The holotype female of *Andrena* (*O.*) *boronensis* (CAS No. 11,274) was collected at Boron, Kern County, California, April 3, 1959 at flowers of *Camissonia campestris* (as *dentata*) by J.W. MacSwain. The holotype female of *A.* (*O.*) *eulobi* (CAS No. 11,277) was collected 14 miles south of San Quintin, Baja California del Norte, Mexico, March 30, 1962, at flowers of *Camissonia* (as *Oenothera*) *crassifolia* by P.H. Raven. Linsley and MacSwain, 1963, cite this locality as 14 miles north of San Quintin, but the label on the holotype clearly has the locality as 14 miles south of San Quintin.

**Distribution.** *Andrena boronensis* occurs in southern California and in Baja California del Norte (Fig. 5). It has been collected from March 2 to August 5 but chiefly from the end of March to early June. In addition to the type material, a total of 422 females and 106 males were examined from localities listed below.

CALIFORNIA. IMPERIAL CO.: Travertine Rock. INYO CO.: Goodale Creek (N of Lone Pine). KERN CO.: Boron; Mojave (and 6 mi. E); Red Rock Canyon; Short Canyon (6.5 mi. NW of Inyokern); Walker Pass Summit (0.7 and 7.2 mi. NW); Weldon (0.5 mi. S). LOS ANGELES CO.: Claremont; Little Rock (and 1 mi. W); Pearlblossom (5 mi. S); Palmdale; Valyermo. RIVERSIDE CO.: Thousand Palms. SAN BERNARDINO CO.: Apple Valley; Barstow (2 mi. W); Desert Springs; Kramer Hills; Salt Wells (7 mi. W). San Diego Co.: Anza-Borrego State Park; Descanso-Alpine; Oak Grove; Pegleg Smith Monument; Shelter Valley. TULARE CO.: Johnsdale. MEXICO. BAJA CALIFORNIA DEL NORTE: Guerro Negro; San Quintin (14 miles N).

**Nest Biology.** Linsley et al. (1964) give the following account of the nesting of this species. "Most burrows of *A. boronensis* were found in or near the borders of hard-packed, unpaved roadbeds. Several were excavated at Little Rock. They were 7 mm in diameter and slanted down from the ground surface at an angle of about 45 degrees to a depth of 11 to 14 cm; from this point they progressed vertically to a depth of 36 to 47 cm and then laterally for 12 to 20 cm where a horizontal cell was placed."

**Floral Records.** *Andrena boronensis* is an oligolege of the genus *Camissonia* (Linsley et al. 1973). It has been collected from flowers of the plants listed below.

*Baccharis viminea*, *Camissonia bistorta*, *C. brevipes*, *C. campestris*, *C. claviformis aurantiaca*, *C. c. claviformis*, *C. crassifolia*, *C. kernensis*, *Coreopsis bigelovii*, *C. californica*, *Cryptantha intermedia*, *Encelia farinosa*, *Ericameria linearifolia*, *Eriophyllum confertiflorum*, *Layia glandulosa*, *Potentilla* sp., *Salix exigua*, *S. lasiolepis*.

### ***Andrena (Onagrاندrena) stagei* Linsley and MacSwain.**

*Andrena (Onagrاندrena) stagei* Linsley and MacSwain, 1962, Pan-Pacific Ent., 38: 52; Linsley, MacSwain, and Raven, 1963, Univ. California Publ. Ent., 33:31, 38.

*Andrena stagei* is known only from the type material and only in the female sex. These females are very similar to those of *boronensis* with sparse punctures on terga 2–4, but have the scopal hairs of the hind tibiae slightly longer and sparser.

**FEMALE: Measurements and Ratios.** N = 1; length, 11.0 mm; width, 3.5 mm; WL, 4.05 mm; FL/FW, 1.04; FOVL/FOVW, 2.81.

**Diagnosis.** Color of vestiture and integument as in *oenotherae* but wings slightly more infumate. Galeae, labral process, clypeal sculpture and pronotum as in *oenotherae*. Vertex above lateral ocellus shorter than one ocellar diameter, ocelli slightly enlarged. Mesoscutum, scutellum, and propodeum sculptured as in *oenotherae*. Metasomal terga 2 and 3 with apical areas with punctures separated mostly by 3 to 5 puncture widths, punctures small to minute, basal areas with punctures separated by 1 to 3 or more puncture widths, surfaces shiny. Thoracic dorsum with long hairs as in *oenotherae*; scopal hairs long, simple, sparse, not hiding surface of tibia at least medially.

**Type Material.** The holotype female and two female paratypes of *Andrena (O.) stagei* (CAS No. 11,280) were collected at Little America (22 miles W of Green River), Sweetwater County, Wyoming, June 20, 1960, at flowers of *Oenothera pallida trichocalyx* by G.I. Stage (Fig. 5). Since this species is known only from the type specimens, no further distribution or floral data are cited.



***Andrena (Onagrandroidrena) chylismiae* Linsley and MacSwain**

*Andrena chylismiae* Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:121–123;

Linsley, MacSwain, and Raven, 1963, Univ. California Publ. Ent., 33:31, 37–38.

*Andrena thorpi* Linsley and MacSwain, 1962, Pan-Pacific Ent., 38:51; Linsley,

MacSwain, and Raven, 1963, Univ. California Publ. Ent., 33:31, 38–39. **New**

**synonymy.**

*Andrena chylismiae* is closely related to *A. oenotherae* which it resembles by the densely punctate metasomal terga but differs by the long sparse tibial scopal hairs of the females and the entirely black vestiture of the males. This species differs from either *stagei* or *boronensis* by the denser metasomal punctation as described below.

**FEMALE: Measurements and Ratios.** N = 20; length, 12–15 mm; width, 3.0–4.5 mm; WL, M =  $4.34 \pm 0.293$  mm; FL/FW, M =  $1.04 \pm 0.004$ ; FOVL/FOVW, M =  $2.96 \pm 0.042$ .

**Diagnosis.** Vestiture black; wing membranes hyaline, slightly infumate, veins dark brown to black; metasomal terga without metallic reflections. Galeae and labral process as in *oenotherae*. Clypeus sculptured as in *oenotherae*. Pronotum without humeral angle or ridge laterally; mesoscutum, scutellum, mesepisternum and propodeum sculptured as in *oenotherae*. Terga 2 and 3 with punctures dense as in as in *oenotherae*. Thoracic dorsum with hairs long as in *oenotherae*; propodeum without corbícula laterally, hairs long and plumose; scopal hairs long, simple sparse, not hiding surface.

**MALE: Measurements and Ratios.** N = 14; length, 11–12 mm; width, 3.0–3.5 mm; WL, M =  $4.15 \pm 0.299$  mm; FL/FW, M =  $1.09 \pm 0.07$ ; FS1/FS2, M =  $1.19 \pm 0.022$ .

**Diagnosis.** Vestiture entirely black; wing membranes hyaline, only slightly infumate, veins dark brown to black; metasomal terga without metallic reflections. Galeae as in female; labral process bidentate; clypeus densely punctate, surface shiny; vertex above lateral ocellus equals about one ocellar diameter; flagellar segment 1 with minimum length about equal to segment 3, slightly longer than segment 2. Pronotum as in *oenotherae* female; mesoscutum and scutellum sculptured as in *oenotherae* female but punctures slightly smaller; propodeum and mesepisternum sculptured as in *oenotherae* female. Metasomal terga 2–5 with apical area punctures separated by one to three puncture widths, lightly shagreened if at all; basal area punctures separated usually by 1 to 2 puncture widths. Metasomal tergum 2 with basal area hairs long as in *oenotherae*; hind tibiae with long sparse hairs along anterior margin as in *oenotherae*. Sternum 7 similar to that of *oenotherae* but with apical lobes slightly narrower and less distinctly hairy; sternum 8 capitate with weak apicomedian emargination, somewhat angular laterally, neck region short, broad (Figs. 45 and 46).

**Type Material.** The holotype female of *Andrena (O.) chylismiae* (CAS No. 6,700) was collected 10 miles S of Reno, Washoe County, Nevada, May 29, 1959, at flowers of *Camissonia* (as *Oenotherae*) *claviformis cruciformis* by P.H. Raven. The holotype female of *A. (O.) thorpi* (CAS No. 11,281) was collected 11 miles N of Winnemucca, Humboldt County, Nevada, June 8, 1961, from flowers of *Oenothera deltoides piperi* by J.W. MacSwain.

**Distribution.** *Andrena chylismiae* is known from California west of the Sierra Nevada Mts., and southern Oregon east to western Wyoming and eastern Utah (Linsley, MacSwain, and Raven, 1963, p. 37) (Fig. 5). It has been collected from May 19 through June 18. A single female supposedly collected in the Santa Catalina Mts. in Pima Co. Arizona by Osler is probably mislabeled (Thorp, 1970) and is not included in the localities listed below. In addition to the types and paratypes, 242 females and 23 males were examined from localities listed below.

CALIFORNIA. INYO CO.: Big Pine; Big Pine Creek (8000 ft. alt.). LASSEN CO.: Ravendale (19 mi. SE). MONO CO.: Benton. NEVADA. EUREKA CO.: Emigrant Pass (4 mi. E); Eureka (2 and 28.5 mi. W. and 7.6, 17.1, 50.2 and 73.3 mi. N). HUMBOLDT CO.: Winnemucca (and 11 mi. N and 10 mi. S). LANDER CO.: Austin (2.5 and 12 mi. E,

9.5 mi. W); Reese River Valley (9.7 and 14.7 mi. W. of Austin; Railroad Pass (3 mi. E). WASHOE CO.: Reno (10 mi. S); Steamboat Springs (10 mi. S of Reno). OREGON. HARNEY CO.: Frenchglen (20 mi. S). UTAH. UINTAH CO.: Brush Creek. WYOMING. LINCOLN CO.: LaBarge (6 mi. S).

**Floral Records.** This species is an oligolege of species of *Camissonia* (Linsley *et al.* 1973). It has been collected at flowers of the plants listed below.

*Camissonia claviformis claviformis*, *C. c. cruciformis*, *C. c. integrrior*, *Melilotus officinalis*, *Oenotherae* sp., *O. deltoides piperi*, *Sisymbrium altissimum*, *Stanleya pinnata*, *Stenotus* (as *Haplopappus*) *acaulis*, *Taraxacum officinale*.

### *Andrena* (*Onagrandrena*) *rozeni* Linsley and MacSwain

*Andrena* (*Melandrena*) *rozeni* Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:164, 166, 168–170; Linsley, MacSwain, and Smith, 1955, Pan-Pacific Ent., 31:176, 179.

*Andrena* (*Onagrandrena*) *rozeni*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:112; Linsley, MacSwain, and Raven, 1963, Univ. California Publ. Ent., 33:11, 36–37; Linsley, MacSwain, and Raven, 1964, Univ. California Publ. Ent., 33:72–73.

*Andrena rozeni* is a distinctive species related to the *deserticola* group of species, but resembling members of the large *oenotherae* group of species. It can be separated from *oenotherae* in either sex by the scutellum having distinct punctures separated by half or more puncture widths especially in the anterior fourth, the interpunctural spaces being dulled by fine tessellation. The tibial scopal hairs are relatively sparse, as in *chylismiae*, but the females of *rozeni* have terga 2–4 more closely punctate basally and the scutellar punctures of *chylismiae* are close set as in *oenotherae*. Rarely the females of *rozeni* have hairs along the posterior margin of the scutellum reddish brown to red, as in some females of *anograe*, but can be separated from the latter by the scutellar sculpturing as described below and the coarser propodeal sculpturing. The male of *rozeni* can be separated from other members of the *oenotherae* group by the pale facial and thoracic hairs together with the sparse scutellar punctures.

**FEMALE: Measurements and Ratios.** N = 20; length, 10–13 mm; width, 3–4 mm; WL, M = 4.05±0.175 mm; FL/FW, M = 1.10±0.004; FOVL/FOVW, M = 3.24±0.053.

**Diagnosis.** Vestiture black except occasionally ochraceous to reddish brown hairs present along posterior border of scutellum; wing membranes hyaline, slightly if at all infumate, veins dark reddish brown to dark brown; metasomal terga without metallic reflections. Galeae, vertex and ocelli as in *oenotherae*. Labral process narrowed apically, with sides concave, apical part about as broad as long and about as broad as base of scape. Clypeus sculptured as in *oenotherae*; vertex above lateral ocellus equals ocellar diameter or slightly less. Pronotum without humeral angle or vertical ridge laterally. Mesoscutum with crowded small punctures separated mostly by half a puncture width or less, surface dulled by fine tessellation. Scutellum punctate, near anterior margin punctures distinctly separated by half to one puncture width, surface finely tessellate. Propodeum sculptured as in *oenotherae*; mesepisternum coarsely punctatorugose except posteromedially where punctures small, obscured by dense tessellation. Terga 2–4 with basal area punctures separated by half to one puncture width or slightly more, surface shiny; apical areas punctate below: basally (basal half to three-fourths), punctures separated mostly by half to two or three puncture widths or more, surfaces shiny. Thoracic dorsum with hairs much longer than width of scape; propodeum without distinct corbicula laterally, hairs long and plumose; scopal hairs long, simple, sparse, not at all hiding surface of tibia.

**MALE: Measurements and Ratios.** N = 20; length, 9–11 mm; width, 2.5–3.0 mm; WL, M = 3.59±0.236 mm; FL/FW, M = 1.17±0.010; FS1/FS2, M = 1.20±0.020.



**Diagnosis.** Vestiture black except as follows: head hairs white except vertex with short to long black hairs, face in narrow zone near eye margin usually with dark hairs, genal area often with dark hairs mixed with the white; thoracic hairs white except pleurae with some dark brown to black hairs ventrally and on lower lateral surfaces; metasomal tergum 1 often with white hairs basally. Wing membranes hyaline, veins dark reddish brown; metasomal terga black, apical areas not translucent. Galeae as in female; labral process bidentate; clypeus densely punctate; vertex above lateral ocellus equals one ocellar diameter or slightly less; flagellar segment 1 as in *oenotherae*; labral process large, bidentate, reflexed. Pronotum as in female; mesoscutum and scutellum as in female but punctures slightly smaller; mesepisternal sculpture as in female; propodeum as in *oenotherae*. Metasomal terga 2–5 sculptured as in female terga 2–4 but punctures slightly sparser. Metasomal tergum 2 with basal area hairs shorter than half length of hairs of tergum 1; hind tibiae with hairs sparse and long as in *oenotherae*. Sternum 7 similar to that of *chylismiae* in shape but with abundant short hairs on apicomedian lobes and apicolaterally; sternum 7 distinctly capitate, apex rounded, neck region narrow, vestiture coarse, long, dense (Figs. 49–50).

**Type Material.** The holotype female of *Andrena (O.) rozeni* (CAS No. 6,708) was collected from near Needles, San Bernardino County, California, March 6, 1930, by E. G. Linsley.

**Distribution.** *Andrena rozeni* is known from southern California, Nevada, Arizona, and Sonora in Mexico (Linsley, MacSwain, and Raven, 1963, pp. 7, 36) (Fig. 3). It has been taken from December 4 through June 23 but chiefly from late February to the end of April. In addition to the holotype, a total of 962 females and 237 males were examined from localities listed below.

ARIZONA. LA PAZ CO.: Vicksburg. MARICOPA CO.: Gila Bend (13 and 32 mi. E). PIMA CO.: Cortaro; Sells (32.8 mi. NE). YUMA CO.: Hope (7 mi. W); Mohawk (9.5 mi. W); Yuma. CALIFORNIA. IMPERIAL CO.: Coyote Wells (3 and 6 mi. W); Kane Springs; Ocotillo; Palo Verde (and 3 mi. S); Yuma Desert. INYO CO.: Eureka Dune (35 mi. ESE of Bigpine); Lone Pine (N of Goodale Creek); Shoshone (5.5 mi. N). KERN CO.: Sand Canyon (3 mi. W of Brown); Walker Pass (1 mi. W). LOS ANGELES CO Co.: Edwards Airforce Base (SW boundary and 1 mi. S); Llano (2 mi. SW). RIVERSIDE CO.: Andreas Canyon; Berdoo Canyon; Blythe (18 mi. W); Boyd Desert Research Center (4 mi. S of Palm Desert); Coachella Valley; Desert Center (4 mi. E); Desert Hot Springs (Whitehouse Canyon); Hopkins Well (2 mi. W); Indio; Joshua Tree Natl. Mon. (Bell Picnic area); La Quinta; Palm Canyon; Palm Desert; Pinyon Crest (12 road mi. SW Palm Desert); Thousand Palms. SAN BERNARDINO CO.: Baker (2 mi. N); Baker Sand Dunes (9 air mi. S, Zzyzx Springs); Cajon Pass; Calico; Essex; Kelso (7 mi. S in Providence Mts.); Kramer Hills; Kramer Junction; Mojave Desert; Needles (and near and 30 mi. S); Salton Sea; Vidal Junction (7 mi. N); Vidal (5 mi. N); Vulcan Mines; Yucca Valley. SAN DIEGO CO.: Borrego (9 mi. E at Coyote Creek); Borrego Palm Canyon, Borrego State Park; Borrego Springs; Borrego Valley (and dunes); Jacumba (5 mi. E); Julian (near Salton Sea); Sentenac Canyon; Tub Canyon (Borrego). NEVADA. CLARK CO.: Searchlight. WASHOE CO.: Sparks (4.5 mi. N); Wadsworth (28 mi. W). MEXICO. SONORA: Sonoyta (50 mi. W and 134 km S).

**Nest Biology.** Females of *A. rozeni* nest in sandy soil (Linsley *et al.* 1963a). They prefer shallow depressions and the base of shaded road cuts as sites to initiate nest construction. Their burrows angle about 45 degrees downward for the first 5 cm or more, descend vertically for about 1 meter and turn horizontally for about 20 cm where a brood cell is constructed. Burrows were commonly started in the afternoon with excavation continuing through the night. Females seem to require more than one night of nest preparation before initiating pollen foraging.

**Floral Records.** *Andrena rozeni* is an oligoledge of plants of crepuscular blooming species of the genus *Camissonia* and has been collected from plants listed below.



*Agoseris glauca*, *Baccharis* sp., *Baileya* sp., *B. multiradiata*, *Brassica* sp., *Camissonia boothii decorticans*, *C. claviformis aurantiaca*, *C. c. claviformis*, *C. c. integrrior*, *C. c. peirsonii*, *C. tanaecetifolia*, *Cryptantha clevelandii*, *C. intermedia*, *Encelia* sp., *E. farinosa*, *Geraea canescens*, *Hyptis emoryi*, *Isomeris arborea*, *Madia rammii*, *Medicago sativa*, *Mirabilis* sp., *Oenothera* sp., *O. deltoides pinnata*, *O. pallida*, (as *latifolia*), *O. piperi*, *O. trichocalyx*, *Sisymbrium altissimum*, *Stanleya* sp., *Taraxacum officinale*.

### *Andrena (Onagrandrena) linsleyi* Timberlake

*Andrena linsleyi* Timberlake, 1937, Pan-Pacific Ent., 13:71–72; Linsley, 1938, Proc. California Acad. Sci., Ser. 4, 23:266, 278.

*Andrena (Melandrena) linsleyi*: Lanham, 1949, Univ. California Publ. Ent., 8:221; Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:165, 166, 170–171; Linsley, MacSwain, and Smith, 1955, Pan-Pacific Ent., 31:176, 179.

*Andrena (Onagrandrena) linsleyi*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:112; Linsley, MacSwain, and Raven, 1963, Univ. California Publ. Ent., 33(1):11–16; Linsley, MacSwain, and Raven, 1964, Univ. California Publ. Ent., 33(2):73.

*Andrena enceliarum* Cockerell, 1937, American Mus. Novs. No. 948, p. 13. **New synonymy.**

*Andrena linsleyi* is a relatively large *Oenothera* bee with sparse, long scopal hairs, a triangular labral process with rounded tip, and relatively weakly sculptured propodeum and mesepisterna. The male of *linsleyi* has the vestiture entirely white. Both sexes are marked by relatively sparsely punctate clypeus, scutellum and mesoscutum as described below.

**FEMALE: Measurements and Ratios.** N = 20; length, 11–14 mm; width, 3.5–4.0 mm; WL, M =  $4.10 \pm 0.145$  mm; FL/FW, M =  $1.12 \pm 0.004$ ; FOVL/FOVW, M =  $3.12 \pm 0.032$

**Diagnosis.** Vestiture black; wing membranes hyaline, not infumate, veins reddish brown to dark brown; metasomal terga black without metallic reflections. Galeae moderately long, dulled by fine shagreening; labral process large, triangular with apex rounded, shiny, sides straight, entire. Clypeus with punctures separated by half to one puncture width or slightly more (especially near apex), with distinct, complete, median, impunctate line, shiny, unshagreened; vertex above lateral ocellus equals distinctly less than one ocellar diameter, never more; ocelli moderately enlarged. Pronotum as in *oenotherae*. Mesoscutum and scutellum with distinct punctures separated by half a puncture width or slightly more, surface dulled by fine shagreening. Propodeum with distinct dorsal surface; dorsal enclosure with relatively fine, irregular rugulae; surfaces outside of enclosure punctate, dulled by tessellation, rugulae extremely fine, if present. Mesepisterna with distinct punctures, especially in lower half, obscured by coarse tessellation. Terga 2–4 with punctures small, separated mostly by half to one puncture width or slightly more, surface shiny; apical areas finely punctate in basal half to two-thirds, punctures separated by half to two puncture widths, surfaces shiny. Thoracic dorsum with hairs longer than width of scape; propodeum without distinct corbicula laterally, hairs long and plumose; scopal hairs extremely long, simple and extremely sparse, not at all hiding surface of tibia.

**MALE: Measurements and Ratios.** N = 20; length, 9–11 mm; width, 2.5–3.0 mm; WL, M =  $3.67 \pm 0.188$  mm; FL/FW, M =  $1.16 \pm 0.009$ ; FS1/FS2, M =  $1.33 \pm 0.020$ .

**Diagnosis.** Vestiture white except hind tibiae with inner surfaces yellow. Wing membranes hyaline, veins dark brown to black; metasomal terga black, without metallic reflections. Galeae as in female; labral process large, emarginate apically, slightly reflexed; vertex above lateral ocellus equals less than one ocellar diameter; flagellar segment 1 longer than segment 2 and usually slightly longer than segment 3. Pronotum as in *oenotherae*

female; mesoscutum with punctures separated mostly by half a puncture width, surface dulled by fine, regular shagreening; scutellum similar but punctures separated by slightly more than half a puncture width, especially anteriorly and surface often somewhat shiny in apical half; propodeum and mesepisterna sculptured as in female. Metasomal terga 2–5 sculptured as in female terga 2–4 but punctures usually slightly more crowded, shiny. Metasomal tergum 2 with basal area hairs short, erect; hind tibiae with outer surface hairs long as in *oenotherae*. Sterna 7 and 8 closely resemble those of *blaisdelli*. Sternum 7 with somewhat blunted apical lobes and relatively weak emargination; sternum 8 distinctly capitate with moderately dense hairs (Figs. 51 and 52).

**Type Material.** The holotype female (CAS No. 14,363) of *Andrena* (*O.*) *linsleyi* was collected 2 miles N of Palm Springs, Riverside County, California, on flowers of *Hyptis emoryi* (not collecting pollen) March 7, 1936, by P.H. Timberlake. The holotype male (AMNH) of *A. (O.) enceliarum* was collected at Dublin, Arizona, March 7, 1937, from flowers of *Encelia* sp. by T.D.A. Cockerell

**Distribution.** *Andrena linsleyi* is known to occur in southern California, southern Nevada, western Arizona and Sonora, and Baja California del Norte in Mexico (Linsley, MacSwain, and Raven, 1963, p. 12) (Fig. 2). It has been collected from February 15 through April 26. In addition to the type material, a total of 1,077 females and 205 males were examined from localities listed below (including localities reported in the literature).

ARIZONA. GRAHAM CO.: Dublin. MOHAVE CO.: Topok (3.5 mi. S). YUMA CO.: Quartzite (12 mi. E). CALIFORNIA. KERN CO.: Boron; California City. IMPERIAL Co.: Glamis (2 mi. N); Kane Springs; Paloverde (3 mi. S). RIVERSIDE CO.: Blythe (18 and 19.4 mi. W); Hopkins Well; Indio; La Quinta; Palm Canyon; Palm Desert; Palm Springs (2 mi. N); Salton Sea; Thousand Palms. SAN BERNARDINO CO.: Apple Valley; Baker (9 mi. S, Zzyzx Springs); Essex (and 2 and 3 mi. S and 10 mi. S), Kelso Dunes; Needles (near); Twenty-Nine Palms (and 29 mi. E). SAN DIEGO CO.: Anza (Coyote Canyon); Borrego, Borrego-Springs; Borrego State Park (Coyote Creek); Borrego Valley (Palm Canyon); Costillo-Borrego; Jacumba (15 mi. E); Ocotillo-Borrego. NEVADA. CLARK CO.: Glendale; Mesquite (8 mi. W); Mormon Mesa; Sandy. MEXICO. SONORA: Sonoyta (81 mi. S). BAJA CALIFORNIA DEL NORTE. Osoyoos (Richter Pass Road).

**Nest Biology.** Nests of *A. linsleyi* are initiated in declivities (Linsley *et al.* 1963a). Their burrows descend vertically from a concentric tumulus.

**Floral Records.** An excellent summary of the floral activities of *Andrena linsleyi* is detailed in Linsley, MacSwain, and Raven (1963, pp. 11–16). This species is an oligolege of *Oenothera*, having been collected most frequently from flowers of *O. deltoides*. It has been collected from flowers of the plants listed below.

*Baileya* sp., *B. pleniradiata*, *Camissonia claviformis aurantiaca*, *C. c. clavaeformis*, *Dithyrea californica*, *Encelia* sp., *C. boothii desertorum*, *Dithyrea californica*, *Encelia* sp., *E. farinosa*, *Geraea canescens*, *Hyptis emoryi*, *Oenothera* sp., *O. deltoides deltoides*, *Palaefoxia arida* (as *linearis*).

### *Andrena (Onagrandroidrena) blaisdelli* Cockerell

*Andrena blaisdelli* Cockerell, 1924, Pan-Pacific Ent., 1:59; Bohart, 1937, Pan-Pacific Ent., 13:54; Linsley, 1938, Proc. California Acad. Sci., Ser. 4, 23:266, 267, 277.

*Andrena (Melandrena) blaisdelli*: Lanham, 1949, Univ. California Publ. Ent., 8:221; Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:164, 166, 167; Linsley, MacSwain, and Smith, 1955, Pan-Pacific Ent., 31:176, 183.

*Andrena (Onagrandroidrena) blaisdelli*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:112; Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:118.



*Andrena blaisdelli* is a small species from southern California closely related and similar to *Andrena furva*. The female of *blaisdelli* can be told from that of *furva* by the longer hairs of the mesosomal dorsum, the broader apical part of the labral process, the shorter vertex, the more finely sculptured mesepisterna and propodeum, and the slightly sparser scopal hairs. The male of *blaisdelli* is one of the species of *Onagrandrena* with the vestiture entirely white. It differs from the male of *furva* by the shorter vertex, the more finely sculptured mesepisterna, and the longer first flagellar segment. Both *furva* and *blaisdelli* have small shiny galeae and can be told by these from all other species of *Onagrandrena*.

**FEMALE: Measurements and Ratios.** N = 20; length 10–12 mm; width, 3.0–3.5 mm; WL, M =  $3.35 \pm 0.135$  mm; FL/FW, M =  $0.98 \pm 0.003$ ; FOVL/FOVW, M =  $3.34 \pm 0.039$ .

**Diagnosis.** Vestiture black; wing membranes hyaline, only slightly infumate, veins dark brown; metasomal terga black without metallic reflections. Galeae short, narrow, shiny, not or only finely shagreened; labral process longer than half length of labrum, sides strongly concave, apical part thick, as broad as base of first flagellar segment or broader, usually distinctly emarginate apically. Clypeus with dense small punctures, without medial impunctate line (or with incomplete line), shiny; vertex above lateral ocellus usually equals slightly less than one ocellar diameter, never more. Pronotum without humeral angle or vertical ridge laterally. Mesoscutum and scutellum densely punctate, punctures small, round, surface dulled by fine tessellation; mesepisternum moderately punctatorugose, dulled by shagreening. Propodeum with distinct dorsal surface, dorsal enclosure irregularly rugulose; surface outside of enclosure moderately coarsely punctatorugose, dull. Tergum 1 with basal area shiny, punctate; terga 2–4 with basal areas with punctures separated mostly by half to one puncture width; apical areas slightly upturned, with basal one-third to one-half with small punctures as dense as in basal area, apical third or half impunctate and often slightly upturned; surfaces shiny. Thoracic dorsum with hairs much longer than width of scape; propodeum without distinct corbicula, internal hairs long, plumose; scopal hairs long, sparse, simple, not fully hiding surface.

**MALE: Measurements and Ratios.** N = 16; length, 8–11 mm; width, 2–3 mm; WL, M =  $3.05 \pm 0.200$  mm; FL/FW, M =  $1.02 \pm 0.004$ ; FS1/FS2, M =  $1.46 \pm 0.029$ .

**Diagnosis.** Vestiture white except some short brown hairs occasionally present on vertex. Wing membranes hyaline, not infumate or only slightly so, veins dark reddish brown. Terga black to dark reddish brown, apical areas often somewhat hyaline. Galeae as in female; vertex above lateral ocellus as in female; flagellar segment 1 with minimum length distinctly longer than segment 2 (about as 1.2 to 1.5:1.0), usually longer than segment 3. Pronotum as in female; mesoscutum and scutellum sculptured as in female; propodeum as in female but dorsal enclosure with irregular rugulae somewhat finer; mesepisterna sculptured as in female. Metasomal terga 2–5 sculptured similar to female terga 2–4 but basal area punctures somewhat sparser, usually separated by half to two puncture widths and apical areas with impunctate rims shorter (usually one-third or less of length of apical area). Metasomal tergum 2 with basal area hairs very short, erect, mediobasally much less than half as long as those of tergum 1; hind tibiae with outer surface hairs moderately long, along anterior margin a few almost as long as dorsal femoral hairs. Sternum 7 somewhat flattened apically with a small apicomedian emargination similar to *omninigra*, but less hairy. Sternum 8 strongly capitate, without apical emargination (Figs. 39 and 40).

**Type Material.** The holotype female (CAS No. 1,708) of *Andrena* (*O.*) *blaisdelli* was collected in San Diego, San Diego Co., California, May 30, 1890, by F.E. Blaisdell.

**Distribution.** *Andrena blaisdelli* is known only from southern California and Baja California del Norte (Linsley, MacSwain, Raven, and Thorp, 1973, p. 28) (Fig. 2). It has been collected from March 10 through August 2, but chiefly from late March through early May. A total of 143 females and 21 males were examined from the localities listed below.

CALIFORNIA. KERN CO.: Woody. LOS ANGELES CO.: Altadena; Claremont; La



Crescenta; La Mirada; Pasadena; Pico Canyon (W of Hwy. 5 and W of Newhall); Tujunga. ORANGE CO.: Costa Mesa. RIVERSIDE CO.: Anza (5 mi. E); Gavilan; Moreno (3 mi. NE); Riverside; Sage (5 mi. S); Temecula (7 mi. E). SAN BERNARDINO CO.: Cajon Pass; Mohave Desert (near Deep Creek). SAN DIEGO CO.: Descanso-Alpine; Lakeside (2 mi. NE); Plum Canyon; San Diego; Sentenac Canyon. SAN LUIS OBISPO CO.: Santa Margarita (5 mi. NE); Simmler (10 mi. W). SANTA BARBARA CO.: New Cuyama (28 mi. NW). TULARE CO.: Fairview (1 mi. S). VENTURA CO.: Gorman (5 mi. S in Hungry Valley). MEXICO. BAJA CALIFORNIA DEL NORTE: La Zapopita, Valle de Trinidad.

**Floral Records.** Although doubtlessly an oligoledge of *Camissonia*, this species has been collected from that plant only a few times. However, several females without floral data have at least a few *Camissonia* pollen grains in their scopae. *Andrena blaisdelli* has been collected from flowers of the plants listed below.

*Camissonia bistorta*, *C. californica*, *C. campestris* (as *dentata*), *Cryptantha* sp., *C. intermedia*, *Eriophyllum* sp., *E. confertiflorum*, *Salix lasiolepis*, *Yucca whipplei*.

### *Andrena (Onagrarendra) deserticola* Timberlake

*Andrena deserticola* Timberlake, 1937, Pan-Pacific Ent., 13:73–74; Linsley, 1938, Proc. California Acad. Sci., Ser. 4, 23:266, 278.

*Andrena (Melandrena) deserticola*: Lanham, 1949, Univ. California Publ. Ent., 8:221; Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:165, 172; Linsley, MacSwain, and Smith, 1955, Pan-Pacific Ent., 31:173, 176, 178, 180, 181, 182–183.

*Andrena (Onagrarendra) deserticola*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:112; Linsley, MacSwain, and Raven, 1964, Univ. California Publ. Ent., 33: 68–69; Davis and LaBerge, 1974, Illinois St. Nat. Hist. Surv. Biol. Notes, No. 95, p. 10.

This small species can be recognized in either sex by the shiny mesoscutum and scutellum. The female is a relatively small bee with entirely black vestiture and relatively dense scopal hairs. The male is a small bee with the vestiture entirely white, without sternal subapical fimbriae and with a well-formed pseudopygidial plate on tergum 6.

**FEMALE: Measurements and Ratios.** N = 20; length, 11–13 mm; width, 3.0–3.5 mm; WL, M =  $3.81 \pm 0.141$  mm; FL/FW, M =  $1.00 \pm 0.004$ ; FOVL/FOVW, M =  $3.33 \pm 0.056$ .

**Diagnosis.** Vestiture entirely black; wing membranes hyaline, slightly infumate apically, veins dark reddish brown to black; metasomal terga black without metallic reflections. Galeae moderately long, shagreened; labral process as in *anograe*. Clypeus densely punctate, without median impunctate line or line incomplete, punctures occasionally slightly sparser near apical margin; vertex above lateral ocellus equals about one ocellar diameter. Pronotum without humeral angle or vertical ridge laterally. Mesoscutum and scutellum with abundant small round punctures separated largely by about one puncture width, surfaces shiny, shagreening sparse and delicate or absent. Propodeum with dorsal enclosure irregularly rugulate; dorsal surface outside of enclosure moderately coarsely punctatorugose, surfaces dulled by fine tessellation or shagreening. Mesepisternum weakly to moderately punctatorugose, dulled by fine tessellation. Terga 2–4 with apical areas punctate in basal half or more, impunctate apically, punctures separated mostly by 1 to 2 puncture widths; basal areas with punctures separated by 1 to 2 puncture widths; surface shiny, shagreening absent or light; pygidial plate blunt, apex broad, rounded. Thoracic hairs long, much longer than width of antennal scape; propodeum without corbicula laterally, hairs all long and plumose; scopal hairs moderately long, simple, moderately abundant and dense, hiding surface of tibia at least partially.

**MALE: Measurement and Ratios.** N = 5; length, about 10 mm; width, about 2.5 mm; WL, M =  $3.43 \pm 0.250$  mm; FL/FW, M =  $1.08 \pm 0.014$ ; FS1/FS2, M =  $1.25 \pm 0.033$ .

**Diagnosis.** Vestiture entirely white; wing membranes hyaline, veins red to dark reddish brown; metasomal terga black without metallic reflections, apical areas somewhat translucent, reddened. Galeae as in female; labral process broad, bidentate, reflexed. Clypeus as in female; vertex above lateral ocellus equals about one ocellar diameter; flagellar segment 1 distinctly longer than segment 2, equal to or longer than segment 3. Pronotum as in female; mesoscutum and scutellum shiny, sculptured as in female, punctures slightly finer; propodeum as in female but dorsal area somewhat more coarsely sculptured; mesepisterna as in female. Metasomal terga 2–5 with apical areas sparsely punctate in basal half or more, punctures separated by 2 to 3 puncture widths or more, basal areas with punctures relatively sparse, separated by 2 to 5 puncture widths, surfaces shiny. Metasomal tergum 2 with basal area hairs relatively long, at least half as long as those of tergum 1; hind tibiae with outer surface hairs long, sparse, almost as long along anterior margin as dorsal femoral hairs. Sterna 7 and 8 similar to those of *linsleyi* but sternum 7 with apical lobes narrower and sternum 8 with neck region shorter (Figs. 53 and 54).

**Type Material.** The holotype female (CAS No. 14,353) of *Andrena (O.) deserticola* was collected at Adelanto (1 mi. S), San Bernardino County, California, May 28, 1932, from flowers of *Baileya multiradiata* by P.H. Timberlake.

**Distribution.** This species is known only from California (Linsley, MacSwain, Raven, and Thorp, 1973, p. 32) (Fig. 2). It has been collected from March 4 through July 28, but chiefly from mid-March through mid-May. In addition to the holotype, a total of 230 females and 12 males were examined from localities listed below.

CALIFORNIA. KERN CO.: Bakersfield (20 mi. E); Boron; Last Chance Canyon, El Paso Mts.; Short Canyon (6.5 mi. NW of Inyokern); Weldon (10 mi. S). LOS ANGELES CO.: Edwards Airforce Base (SW boundary); Little Rock (1 mi. W); Palmdale (and 2 mi. N); Pearblossom (5 mi. N at Lovejoy Buttes). RIVERSIDE CO.: Joshua Tree Natl. Mon.; Kramer Junction (on county line). SAN BENITO-FRESNO CO.: Big Panoche Creek. SAN BERNARDINO CO.: Adelanto (1 mi. S). SAN DIEGO CO.: Descanso-Alpine.

**Nest Biology.** Burrows of *A. deserticola* at two sites in Short Canyon consisted of aggregations of about a dozen nests on alluvial fans at the upper end of the canyon and near the lower wash. Burrows had vertical entrances, diameters of 6–7 mm, and were about 60 cm deep.

**Floral Records.** *Andrena deserticola* is an oligolege of plants of the genus *Camissonia*. Linsley, MacSwain, and Raven (1964, pp. 68–69) should be consulted for details on floral preferences, as well as other biological notes. This species has been collected from flowers of the plants listed below.

*Baileya multiradiata*, *C. pallida*, *Camissonia* sp., *C. boothii decorticans*, *C. campestris*, *C. claviformis*, *C. kernensis*, *Coreopsis* sp., *C. bigelovii*, *C. californica*, *Cryptantha intermedia*, *Oenothera* (= *Camissonia*?) sp.

### *Andrena (Onagrandrena) nevadae* Linsley and MacSwain

*Andrena (Onagrandrena) nevadae* Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:125–126; Linsley, MacSwain, and Raven, 196, Univ. California Publ. Ent., 33:31, 39.

*Andrena nevadae* is a large black bee known from only the female holotype and one female paratype collected in Nevada. These bees have long, simple, sparse scopal hairs similar to those of *Andrena linsleyi* Timberlake. However, *nevadae* can be separated from *linsleyi* by the shiny mesoscutum and scutellum and by the more coarsely sculptured propodeum. The female of *nevadae* is readily separated from the female of *deserticola* by the sparse scopal hairs and coarsely sculptured propodeum.



**FEMALE: Measurements and Ratios.** N = 1; length, about 13 mm; width, about 4 mm; WL, 4.94 mm; FL/FW, 1.04; FOVL/FOVW, 3.00.

**Diagnosis.** Vestiture entirely black; wing membranes hyaline, slightly infumate apically, veins dark reddish brown to black; metasomal terga black without metallic reflections. Galeae as in *anograe*; labral process triangular, with straight sides, apex thickened to form small knob. Clypeus and vertex as in *deserticola*. Pronotum without humeral angle or vertical ridge laterally. Mesoscutum and scutellum sculptured as in *deserticola*, shiny. Propodeum (Fig. 16) with dorsal enclosure coarsely rugulate, surface outside of enclosure (Fig. 16) moderately coarsely punctatorugose, dulled by fine shagreening. Mesepisterna punctatorugose, surface dulled by shagreening. Metasomal terga 2–4 with apical areas punctate in basal two-thirds, punctures separated by half to one puncture width or slightly more; basal areas with punctures separated mostly by one to two puncture widths; surfaces shiny, shagreening sparse and delicate or absent. Thoracic dorsum with hairs long, much longer than width of antennal scape; propodeum without corbicula laterally, hairs all long and plumose; scopal hairs very long, simple, extremely sparse, not at all hiding surface of tibia.

**Type Material.** The holotype female (CAS No. 6,705) of *nevadae* was collected 1.8 miles west of Pancake Summit, White Pine County, Nevada, June 24, 1959, at flowers of *Camissonia* (as *Oenothera*) *claviformis integrrior* by J.W. MacSwain. A female paratype was collected from 28.5 miles west of Eureka, Eureka County, Nevada, June 8, 1960, at flowers of *Stanleya pinnata* by J.W. MacSwain (Fig. 2).

### *Andrena (Onagrarendra) raveni* Linsley and MacSwain

*Andrena (Onagrarendra) raveni* Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:118–121; Linsley, MacSwain, and Raven, 1963, Univ. California Publ. Ent., 33:31–36.

*Andrena raveni* is very distinctive in both sexes because metasomal terga 1–5 have relatively strong, metallic, bluish or violaceous reflections. The only other species of this subgenus with such reflections is *Andrena vanduzeei* in which the metallic reflections are very much subdued and are strongest on terga 4 and 5 (and 6 in the male sex).

**FEMALE: Measurements and Ratios.** N = 20; length, 11–13 mm; width, 3.0–3.5 mm; WL, M = 4.04±0.170 mm; FL/FW, M = 1.05±0.008; FOVL/FOVW, M = 3.07±0.066.

**Diagnosis.** Vestiture black; wing membranes hyaline, yellowish, slightly infumate; veins dark reddish brown to black; metasomal terga black with dark blue metallic reflections, apical areas, especially on terga 5 and 6, often with violaceous reflections. Galeae as in *oenotherae* but dulled by fine dense tessellation; labral process as in *oenotherae* but apical part slightly thicker, equals width of base of scape or slightly broader, apex usually slightly emarginate. Clypeus with punctures small, round, dense, separated by half a puncture or less, without median impunctate line, shiny; vertex above lateral ocellus equals about one ocellar diameter or slightly less. Pronotum as in *oenotherae*. Mesoscutum densely punctate, punctures separated by half a puncture width or less, interpunctural surface moderately shiny posteriorly or dull, reticular shagreening fine; scutellum similar but punctures denser and moderately shiny only near anterior margin. Propodeum sculptured as in *oenotherae*; mesepisterna distinctly punctured below, punctures crowded, surface dulled by fine tessellation. Terga 2–4 with apical areas punctate except in narrow apical margin, punctures separated mostly by one to three puncture widths, basal area punctures separated mostly by half to one puncture width, surfaces shiny. Thoracic dorsum with hairs much longer than width of scape; propodeum without distinct corbicula laterally, hairs long, plumose; scopal hairs long, simple, sparse.



**MALE: Measurements and Ratios.** N = 20; length, 10–12 mm; width, 2–3 mm; WL, M =  $3.59 \pm 0.249$  mm; FL/FW, M =  $1.10 \pm 0.006$ ; FS1/FS2, M =  $1.39 \pm 0.017$ .

**Diagnosis.** Vestiture black except as follows: vertex with long white hairs, rarely face below ocelli with a few to several pale hairs; mesoscutum and scutellum with white hairs; propodeum without white or with a few on each side anteriorly; mesepisterna entirely black or with a few pale hairs intermixed; metasomal tergum 1 often and tergum 2 occasionally with basal area hairs white in part or nearly entirely. Wing membranes hyaline, slightly infumate, yellowish, veins dark reddish brown; metasomal terga with metallic, bluish or violaceous reflections. Galeae and vertex as in female; labral process large, bidentate; flagellar segment 2 longer than either segment 1 or segment 2. Pronotum as in *oenotherae*; mesoscutum and scutellum sculptured as in female; propodeum as in female; mesepisternum dull, punctatorugulose and finely tessellate. Metasomal terga 2–5 sculptured as in female terga 2–4 but basal area punctures sparser, separated mostly by one to two puncture widths or slightly more, apical areas with apical impunctate rim broader than in female, surfaces shiny. Metasomal tergum 2 with basal area hairs long, mediobasally half as long as those of tergum 1 or longer; hind tibiae with outer surface hairs long, sparse, as in *oenotherae*. Sternum 7 with apicomedian lobes flattened apically as in *blaisdelli* but apicomedian emargination much deeper; sternum 8 with apex weakly capitate, shallowly emarginate apicomediaally, with neck region broad and hairs dense (Figs. 55 and 56).

**Type Material.** The holotype female (CAS No. 6,707) of *Andrena (O.) raveni* was collected from 9.5 mi. W of Austin, Lander Co., Nevada, June 7, 1959, visiting *Camissonia* (as *Oenotherae*) *claviformis integrrior* flowers by J.W. MacSwain.

**Distribution.** *Andrena raveni* is known from California, Idaho, Nevada, Oregon, Utah, and Washington (Fig. 4). It has been collected from May 3 through July 16 but mainly in May and June. In addition to the holotype, a total of 772 females and 79 males were examined from localities listed below.

CALIFORNIA. LASSEN CO.: Hallelujah Junction; Madeline (0.5 mi. N); Ravendale (2 mi. N, 2.4 mi. NW, 3.5 mi. S and 19 mi. SE); Termo (5.5 and 6.5 mi. N). MONO CO.: Benton Inspection Sta. SISKIYOU CO.: Lake Shastina (1 mi. NE); Macdoel; Tulalake (5 mi. S). TRINITY CO.: Long Ridge. (South of Zenia). NEVADA. EUREKA CO.: Emigrant Pass (4 mi. E and 22 mi. W); Eureka (28.5, 33.8, 36.2 and 37 mi. W; 7.6, 17.1, 50.2, 70.8 and 73.3 mi. N). HUMBOLDT CO.: Golconda; Winnemucca (11 mi. N). LANDER CO.: Austin (9.5, 9.7, 11, 14.5 and 14.7 mi. W); Austin Summit (2.5 and 12 mi. E); Railroad Pass (3 mi. E). WASHOE CO.: Reno (10 mi. S); Steamboat Springs (10 mi. S of Reno). OREGON. HARNEY CO.: Fields (10.7 mi. S); Narrows (9 mi. S). KLAMATH CO.: Bonanza (NE of Round Prairie). LAKE CO.: Hart's Moutnain (1.2 mi. W of Antelope Refuge HQ). MALHEUR CO.: Harper (3 mi. SW). MORROW CO.: Boardman Bomb Range; Irrigon. SHERMAN CO.: Meryhill Ferry (3 mi. E of Briggs). UMATILLA CO.: Umatilla. WASCO CO.: The Dalles (7 mi. E). UTAH. TOOELE CO.: Tooele (3.6 mi. S). WASHINGTON. ADAMS CO.: Ritzville (4 mi. N).

**Nest Biology.** Linsley *et al.* give the following short account of the nest of *A. raveni*. "Burrows of *A. raveni* are excavated in loose sandy soil and the entrances are commonly located in surface irregularities. The burrow entrance is vertical and surrounded by a large tumulus."

**Floral Records.** *Andrena (O.) raveni* is an oligolege of the genus *Camissonia* and has been collected from the following plants.

*Agoseris glauca*, *Camissonia claviformis citrina*, *C. c. claviformis*, *C. c. cruciformis*, *C. c. integrrior*, *C. tanacetifolia*, *Euphorbia* sp., *Heterotheca* (as *Chrysopsis*) *villosa*, *Madia ramii*, *Oenotherae alyssoides*, *O. deltoides piperi*, *O. pallida* (and as *latifolia*), *Sisymbrium altissimum*, *S. officinale*, *Stanleya pinnata*, *Taraxacum officinale*, *Thelypodium laciniatum*.

*Andrena (Onagrarendra) vanduzeei* Linsley

*Andrena vanduzeei* Linsley, 1938, Proc. California Acad. Sci., ser. 4, 23:266, 267, 280–281.

*Andrena (Melandrena) vanduzeei*: Lanham, 1949, Univ. California Publ. Ent., 8:221; Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:172; Linsley, MacSwain and Smith, 1955, Pan-Pacific Ent., 31:176.

*Andrena (Onagrarendra) vanduzeei*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:112.

*Andrena vanduzeei* is a small species in which the metasomal terga often show weak metallic reflections (especially terga 4 and 5 of the female and terga 4–6 of the male). The female is marked also by moderately shiny mesoscutum, moderately dense scopal hairs, and an impunctate, narrow, median, clypeal line. The male has dark hairs mixed with the white on the mesoscutum, the first two metasomal terga usually with pale hairs and few pale hairs on the head.

**FEMALE: Measurements and Ratios.** N = 10; length, 10–11 mm; width, about 3 mm; WL, M =  $3.86 \pm 0.158$  mm; FL/FW, M =  $1.05 \pm 0.004$ ; FOVL/FOVW, M =  $3.26 \pm 0.084$ .

**Diagnosis.** Vestiture entirely black; wing membranes hyaline, yellow, moderately infumate, veins dark reddish brown to dark brown; metasomal terga black with extremely weak metallic reflections especially on apical areas of terga 4 and 5, reflections usually violaceous. Galeae as in *oenotherae*; labral process with sides concave as in *oenotherae* but apical part short and broad, at least as broad as base of scape. Clypeus with punctures dense except medially near apical margin and usually with complete, narrow, impunctate midline; vertex above lateral ocellus equals about one ocellar diameter or slightly less. Pronotum as in *oenotherae*. Mesoscutum as in *oenotherae* but interpunctural shagreening light, moderately shiny at least posteromedially; scutellum often shiny along anterior margin. Propodeum finely or moderately finely punctatorugose, surface dulled; mesepisterna with shallow but distinct punctures, not punctatorugose, interpunctural space dulled by fine tessellation. Terga 2–4 with apical area punctures minute, separated mostly by two to four puncture widths, apical rim impunctate, basal areas with punctures separated by half to one or two puncture widths, surfaces shiny; pygidial plate V-shaped with narrowly rounded or pointed apex. Thoracic dorsum with hairs much longer than width of scape; propodeum without distinct corbicula laterally, hairs long and plumose; scopal hairs long, simple, moderately abundant.

**MALE: Measurements and Ratios.** N = 17; length 9–10 mm; width, 2.0–2.5 mm; WL, M =  $3.36 \pm 0.218$  mm; FL/FW, M =  $1.10 \pm 0.004$ ; FS1/FS2, M =  $1.29 \pm 0.015$ .

**Diagnosis.** Vestiture black except as follows: clypeus with hairs in apicomedial band white, occasionally white hairs extend to base along midline but always less than 50% of clypeal hairs pale; vertex with pale hairs; genae occasionally with several pale hairs especially below; mesoscutum and scutellum with pale hairs but black hairs present posteromedially on mesoscutum and medially on scutellum; propodeum often with pale hairs dorsally; pleural areas rarely with pale hairs; terga 1 and 2 with basal area hairs pale or largely so. Wing membranes hyaline, only slightly infumate; metasomal terga (especially terga 4–6 often with weak metallic reflections, especially apically. Galeae as in female; labral process bidentate, reflexed; clypeus with dense round punctures, with weak median impunctate line, especially in apical half, surface shiny; vertex above lateral ocellus equals about one ocellar diameter; flagellar segment 1 longer than segment 2 but about equal in length to segment 3. Pronotum as in *oenotherae* female; mesoscutum and scutellum as in female, but punctures smaller and slightly sparser; propodeum and mesepisternum sculptured relatively weakly, much as in female. Metasomal terga 2–5 sculptured as in female



terga 2–4 but punctures somewhat sparser and apical area punctures often restricted to basal half of apical area. Metasomal tergum 2 with basal area hairs long, mediobasally half as long as those of tergum 1 or longer; hind tibiae with outer surface hairs long, sparse, along anterior margin some hairs almost as long as dorsal femoral hairs. Sternum 7 with apicomedian lobes similar to those of *deserticola*, not flattened apically as in *raveni*, hairs sparse, weak; sternum 8 with apex flattened, not markedly capitate, moderately densely hairy (Figs. 57 and 58).

**Type Material.** The holotype female (CAS No. 4,543) of *Andrena (O.) vanduzeei* was collected from Huntington Lake, Fresno Co., California, July 4, 1919, by E.P. Van Duzee.

**Distribution.** *Andrena vanduzeei* is known to occur only in the high Sierra region of California (Fig. 4). It has been taken from April 10 through August 11, but mainly in June and July. In addition to the holotype, a total of 22 females and 22 males were examined from localities listed below.

CALIFORNIA. ALPINE CO. EL DORADO CO.: Echo Lake; Ice House Road (5 mi. N); Phillips. FRESNO CO.: Cherry Gap Summit; Huntington Lake; Shaver Lake; Sulphur Meadow. PLUMAS CO.: Buck. TULARE CO.: General Grant Grove and Giant Forest Grove, Sequoia Natl. Park. TUOLUMNE CO.: Mill Creek Camp; Strawberry.

**Floral Records.** *Andrena vanduzeei* was collected from only a few species of plants; therefore, little is known concerning its flower preferences. Pollen in its pollen collecting hairs indicate that it probably is an oligolege of *Onagraceae*, presumably *Gayophytum*, based on its late flight period, distribution, and limited flower records. It has been collected from flowers of *Gayophytum diffusum*, *G. d. parviflorum*, *Potentilla* sp., and *Rhamnus* sp.

### *Andrena (Onagrandrena) rubrotincta* Linsley

*Andrena rubrotincta* Linsley, 1938, Proc. California Acad. Sci., ser. 4, 23:266, 278–279.

*Andrena (Melandrena) rubrotincta*: Lanham, 1949, Univ. California Publ. Ent., 8:321; Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:165, 170; Linsley, MacSwain, and Smith, 1955, Pan-Pacific Ent., 31:176.

*Andrena (Onagrandrena) rubrotincta*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:112; Linsley and MacSwain, 1961, Pan-Pacific Ent., 37:128; Linsley, MacSwain, and Raven, 1963, Univ. California Publ. Ent., 33:16–18.

*Andrena rubrotincta* is the first of four species described below that are marked in both sexes by having a well-formed pronotal humeral angle and lateral ridge. The lateral ridge, especially in the females, is not sharply formed but somewhat rounded and the humeral angle is not strongly ear-shaped or triangular as in other subgenera of *Andrena* but are distinct nonetheless. The female of *rubrotincta* can be told from the other species with pronotal humeral angles by the black vestiture and the mesoscutum being dulled by shagreening. The male of *rubrotincta* differs from other members of this group by the lack of a subapical mandibular tooth and the mesoscutum being shagreened.

**FEMALE: Measurements and Ratios.** N = 20; length, 11–13 mm; wing length, 3–4 mm; WL, M =  $4.48 \pm 0.166$  mm; FL/FW, M =  $1.04 \pm 0.006$ ; FOVL/FOVW, M =  $3.04 \pm 0.052$ .

**Diagnosis.** Vestiture dark reddish brown to dark brown; wing membranes hyaline, not at all infumate, veins dark red to dark reddish brown; metasomal terga piceous, without metallic reflections. Galeae as in *oenotherae*; labral process large, triangular with blunt tip, often slightly emarginate apically, sides usually straight, rarely concave (Fig. 20); vertex above lateral ocellus short, equals about half an ocellar diameter. Clypeus with small round punctures separated mostly by half a puncture width or slightly more, with narrow median impunctate line. Vertex above lateral ocellus equals about half an ocellar diameter; ocelli not enlarged. Pronotum with distinct humeral angle and dorsoventral ridge laterally (Fig.



18). Mesoscutum with small round punctures separated mostly by half a puncture width or more, surface dulled by fine reticular shagreening; scutellum similar but punctures slightly denser. Propodeum with dorsal surface distinct, dorsal enclosure weakly sculptured, finely tessellate; surface outside of enclosure not punctatorugose, with scattered obscure punctures and fine reticular shagreening dulling surface; 2–4 with apical areas punctate except narrow rim, punctures separated mostly by one to three puncture widths, basal areas with punctures separated mostly by one to two puncture widths, surfaces shiny. Thoracic dorsum with hairs longer than width of scape; propodeum without distinct corbicula laterally, hairs long and plumose; tibial scopal hairs long, simple, sparse, scarcely hiding surface.

**MALE: Measurements and Ratios.** N = 20; length, 9–11 mm; width, 2.0–2.5 mm; WL, M =  $3.74 \pm 0.173$  mm; FL/FW, M =  $1.06 \pm 0.005$ ; FS1/FS2, M =  $1.32 \pm 0.022$

**Diagnosis.** Vestiture pale, white to pale ochraceous, except on vertex and along inner margins of eyes usually brown; wings hyaline, slightly infumate apically, veins dark reddish brown to black; metasomal terga black or piceous, without metallic reflections. Galeae as in *oenotherae*; labral process large, trapezoidal with median emargination (not strongly bidentate), curved but not strongly reflexed; mandibles decussate, without subapical tooth (Fig. 17). Clypeus with punctures small, irregularly separated by half to one puncture width, usually with median impunctate line, shiny; vertex above lateral ocellus equals less than one ocellar diameter and usually slightly more than half an ocellar diameter; genal area twice as broad as eye in profile; flagellar segment 1 equal to or slightly longer than segment 3, distinctly longer than 2. Pronotum as in female (Fig. 19). Mesoscutum and scutellum as in female but punctures slightly sparser and surface often slightly shiny, shagreening delicate but present; propodeum and mesepisternum sculptured as in female but propodeum with dorsal enclosure slightly more coarsely rugulate. Terga 2–5 with apical areas as in female terga 2–4 but punctures smaller and slightly sparser; basal areas similar to female. Metasomal tergum 2 with basal area hairs short, mediobasally less than half as long as those of tergum 1; hind tibiae with outer surface hairs long, sparse, along anterior margin some almost as long as dorsal femoral hairs. Sternum 7 similar to that of *vanduzeei*, vestiture sparse, weak; sternum 8 with apex broad, gently emarginate, neck region strongly hairy (Figs. 59 and 60).

**Type Material.** The holotype female (CAS No. 4,235) of *Andrena* (*O.*) *rubrotincta* was collected from the Colorado Desert near Needles, San Bernardino Co., California, March 6, 1930, by E.G. Linsley.

**Distribution.** *Andrena rubrotincta* is known from southern California, Nevada, and western Arizona (Linsley, MacSwain, and Raven, 1963, p. 17) (Fig. 6). We also have seen a specimen from Utah. It has been collected from February 1 through May 9 but chiefly in March and April. In addition to the holotype, a total of 78 females and 26 males were examined from localities listed below.

ARIZONA. MOJAVE CO.: Cane Springs; Havasu City; Kingman (8 mi. N and 32 mi. NW); Topock. CALIFORNIA. IMPERIAL CO.: Coyote Wells (6 mi. W); Painted Canyon (4.6 mi. NE Mecca). KERN CO.: Short Canyon (6 and 6.5 mi. NW Inyokern); Walker Pass (1 mi. W). RIVERSIDE CO.: Boyd Desert Research Center (4 mi. S. Palm Desert); Coyote Creek; Deep Canyon Recreation Area; Desert Center (4 mi. E); Desert Hot Springs (4.5 mi. NW); Elsinore (4 mi. E); Indio; Joshua Tree Natl. Mon.; La Quinta; Palm Desert; Thousand Palms. SAN BERNARDINO CO.: Kelso (7 mi. S in Providence Mountains); Needles (near, 9 mi. S and 15 mi. SE). SAN DIEGO CO.: Borrego; Jacumba (5 mi. E). NEVADA. CLARK CO.: Glendale (and 1.6 mi. E and 6 mi. NE); Mesquite (4 mi. W); Mormon Mesa; Overton. UTAH. WASHINGTON CO.: Virgin (3 mi. W).

**Floral Records.** *Andrena* (*A.*) *rubrotincta* is an oligoledge of plants of the genus *Camissonia* (as *Oenothera* in earlier publications) and has been collected from flowers of the plants listed below.

*Baileya* sp., *Camissonia* sp., *Camissonia b. brevipes*, *C. b. pallidula*, *C. claviformis*, *C. c. aurantiaca*, *C. (as Oenothera) parryi*, *Hyptis emoryi*, *Lesquerella* sp., *Oenothera* sp., *Phoradendron californicum*, *Salix* sp., *Tamarix gallica*.

***Andrena (Onagrandrena) mojavensis* Linsley and MacSwain**

*Andrena (Melandrena) mojavensis* Linsley and MacSwain, 1955, Pan-Pacific Ent., 31:165, 171–172; Linsley, MacSwain, and Smith, 1955, Pan-Pacific Ent., 31:173, 174, 176, 178, 179–181, 182, 183.

*Andrena (Onagrandrena) mojavensis*: Linsley and MacSwain, 1956, Pan-Pacific Ent., 32:112; Linsley, MacSwain, and Raven, 1964, Univ. California Publ. Ent., 33:65–67; Davis and LaBerge, 1975, Illinois Nat. Hist. Survey, Biol. Notes, No. 95, p. 10.

*Andrena mojavensis* is a large bee closely related to *rubrotincta*. The female of *mojavensis* has the mesoscutum and scutellum shiny. The male of *mojavensis* also has a shiny mesoscutum and scutellum and has a distinct subapical mandibular tooth.

**FEMALE: Measurements and Ratios.** N = 20; length, 13–14 mm; width, 3–4 mm; WL, M =  $4.50 \pm 0.081$  mm; FL/FW, M =  $1.01 \pm 0.005$ ; FOVL/FOVW, M =  $2.96 \pm 0.041$ .

**Diagnosis.** Vestiture dark brown to black; wing membranes hyaline, veins dark reddish brown to dark brown; metasomal terga piceous, not metallic. galeae as in *oenotherae*; labral process and vertex as in *rubrotincta*. Clypeus sculptured as in *rubrotincta*. Vertex and ocelli as in *rubrotincta*. Pronotum with humeral angle and lateral ridge. Mesoscutum and scutellum punctate as in *rubrotincta* but surfaces shiny, shagreening delicate and largely peripheral, if present. Propodeum and mesepisterna sculptured as in *rubrotincta*. Terga 2–4 with apical areas sculptured as in *rubrotincta* but apical impunctate rim broader, often equal to half of apical area and punctures smaller and sparser; basal areas with punctures sparse and minute, separated mostly by three to five puncture widths; surfaces shiny. Thoracic hairs and pollen-collecting hairs as in *rubrotincta*.

**MALE: Measurements and Ratios.** N = 20; length, 9–11 mm; width, 2–3 mm; WL, M =  $3.85 \pm 0.279$  mm; FL/FW, M =  $1.00 \pm 0.004$ ; FS1/FS2, M =  $1.24 \pm 0.016$ .

**Diagnosis.** Vestiture pale, yellowish or ochraceous, darker on face and thoracic dorsum, usually brown on vertex and along inner margins of eyes, occasionally some brown hairs on gena near outer margin of eye; wing membranes hyaline, veins reddish brown to dark brown; metasomal terga brown to black but apical areas hyaline, yellow to reddish brown. Galea as in *oenotherae*; labral process as in *rubrotincta*; mandibles decussate, with more or less distinct subapical tooth; clypeus, vertex, genal area and flagellar segments as in male of *rubrotincta*. Pronotum as in female. Mesoscutum and scutellum sculptured much as in female, surfaces shiny; propodeum and mesepisterna sculptured as in female. Terga 2–5 sculptured as in female terga 2–4 but apical areas with punctures minute and often barely visible. Metasomal tergum 2 with basal area hairs short, as in *rubrotincta* male; hind tibiae with hairs as in *rubrotincta*. Sterna 7 and 8 similar to those of *rubrotincta* but sternum 7 with denser hairs and sternum 8 with smaller apical lobes and dense vestiture (Figs. 61 and 62).

**Type Material.** The holotype female (CAS No. 6,704) of *Andrena (O.) mojavensis* was collected from Short Canyon, 6.5 mi. NW of Inyokern, Kern Co., California, April 13, 1954 from flowers of *Camissonia campestris* (as *Oenothera dentata* var. *johnstonii*) by James M. Linsley.

**Distribution.** *Andrena mojavensis* is known to occur only in northeastern Kern County in California (Fig. 6). It has been collected from March 19 through April 26. In addition to the type material, a total of 470 females and 43 males were examined from localities listed below.



CALIFORNIA. KERN CO.: Brown (3 mi. W in Sand Canyon); Jawbone Canyon; Short Canyon (6.5 mi. NW of Inyokern); Walker Pass (1 mi. W).

**Nest Biology.** The following notes are from Linsley *et al.* (1964). "Burrows of *A. mojaviensis* are constructed in the coarse granitic sand of the upper slopes of Short Canyon and in the finer sand of the upper washes near these slopes. Those on the upper slopes penetrated to an underlying layer of decomposing granite at depths of 60 to 75 cm; in the finer sand of the washes and alluvial fans the only one found was 60 cm deep. They had vertical entrances and diameters averaging almost 8 mm. All were scattered over a wide area with no tendency toward aggregations."

**Floral Records.** This species is an oligoecologist of species of *Camissonia* (primarily *C. kernensis*) and has been collected from flowers of plants listed below (including records from the literature).

*Camissonia campestris*, *C. claviformis claviformis*, *C. kernensis*, *Coreopsis bigelovii*, *Cryptantha* sp., *Dithyrea californica*.

### *Andrena (Onagrandra) camissoniae* Linsley and MacSwain

*Andrena (Onagrandra) camissoniae* Linsley and MacSwain, 1968, Pan-Pacific Ent., 44:144-145; Linsley, MacSwain, Raven, and Thorp, 1973, Univ. California Publ. Ent., 71:27, 29.

*Andrena camissoniae* is a moderately large bee related to *rubrotincta* and *mojavensis* but marked by the pale buff or ochraceous vestiture in both sexes. In addition both sexes have the propodeum somewhat more coarsely sculptured than in *rubrotincta* or *mojavensis* and slightly darker wing membranes. Since the male has not been previously described, a complete description is given below.

**FEMALE: Measurements and Ratios.** N = 2; length, 10-11 mm; width, 3.0-3.5 mm; WL, 3.67-4.05 mm; FL/FW, 1.00-1.01; FOVL/FOVW, 3.28-3.31.

**Diagnosis.** Vestiture pale, yellowish to ochraceous, darker on face and dorsum of thorax, facial foveae with white tomentum in lower half or slightly more and reddish brown in upper half or less; wing membranes hyaline but slightly infumate, yellowish; metasomal terga piceous, without metallic reflections. Galeae as in *oenotherae*; labral process large, sides concave, apical part as broad as base of scape or slightly broader (Fig. 18); vertex above lateral ocellus equals less than one ocellar diameter. Clypeus with small round punctures separated mostly by less than half a puncture diameter, with very narrow impunctate median line. Vertex above lateral ocellus equals about half an ocellar diameter; ocelli not enlarged. Pronotum as in *rubrotincta*. Mesoscutum and scutellum with small round punctures separated largely by about half a puncture width, interpunctural surfaces dulled by fine reticular shagreening. Propodeum with dorsal surface distinct; dorsal enclosure moderately sculptured (Fig. 21), often with complete median rugula and at least basal half rugulate; surface outside of enclosure with some rugulae and relatively coarse punctures (not punctatorugose); surfaces finely tessellate; mesepisternum extremely shallowly punctatorugose, bottoms of punctures dulled by fine shagreening. Metasomal terga 2-4 with apical areas with minute punctures separated by three to five puncture widths, apical rim impunctate; basal areas punctures larger, separated mostly by two to three puncture widths; surfaces shiny. Thoracic dorsum with hairs longer than scape width; propodeum with lateral corbícula not distinctly formed, internal hairs plumose; tibial scopal hairs long, simple, sparse, scarcely hiding surface; metasomal terga 2-4 with basal area hairs erect, short (distinctly shorter than apical area hairs).

**MALE: Measurements and Ratios.** N = 3; length, 9-10 mm; width, 2.5-3.0 mm; WL, M = 3.06±0.845 mm; FL/FW, M = 1.00±0.003; FS1/FS2, M = 1.30±0.035.



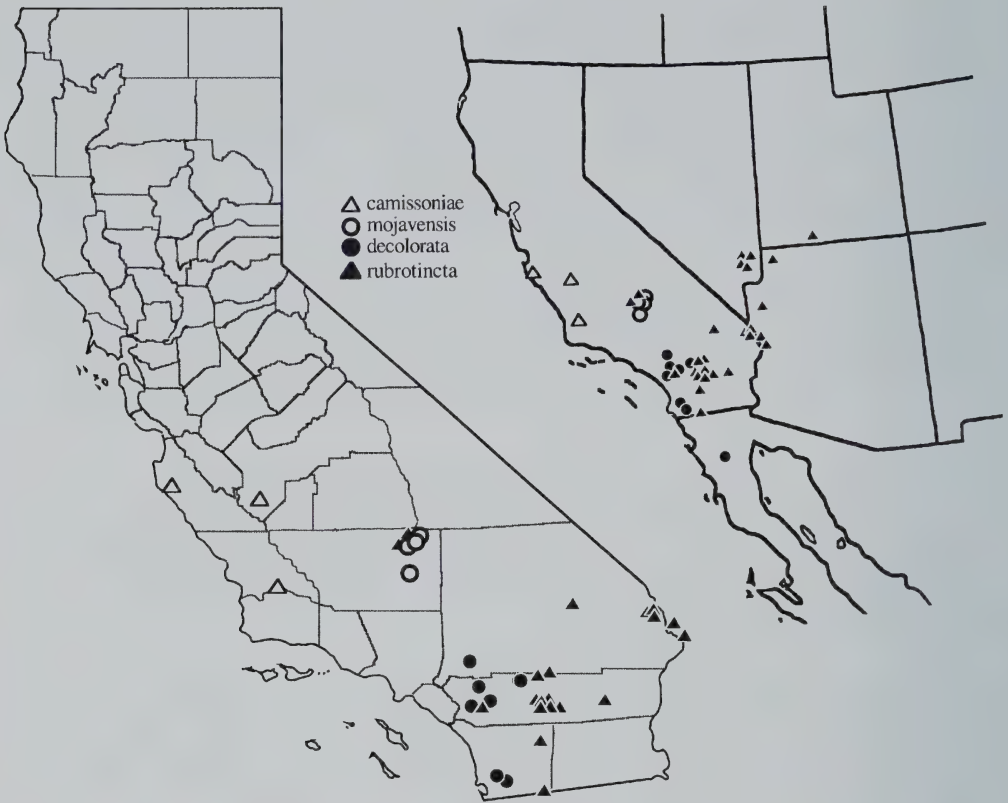


Fig. 6. Maps showing the distributions of *Andrena camissoniae*, *A. mojavenensis*, *A. decolorata*, and *A. rubrotincta*.

**Integumental Color.** Black except as follows: mandible with apical fourth rufescent; terga with apical areas translucent, rufescent; antennal scape reddish brown below; wing membranes hyaline, slightly infumate, yellowish, veins red to reddish brown.

**Structure.** Antennae in repose just reaching scutellum; scape length equals first three flagellar segments; flagellar segment 1 longer than 2, about as long as 3, all flagellar segments longer than broad. Eyes each about three times as long as broad. Mandible with small, subapical inner tooth present (Fig. 22). Galeae long, dulled by fine tessellation. Maxillary palpus long, segmental ratio about as 1.0:0.85:1.0:0.85:0.85:0.85. Labial palpus with ratio about as 1.0:0.8:0.5:0.4. Labral process large, reflexed, strongly bidentate with U-shaped median emargination (Fig. 22). Clypeus short, punctures round, separated by half to one puncture width, surface shiny, without impunctate median line. Supraclypeal area moderately shiny, with small, close-set punctures. Face below ocelli with longitudinal rugae and interrugal punctures. Vertex above lateral ocellus equals about one ocellar diameter or slightly less. Genal area in profile twice as broad as eye, with posterior angle just below midline, surface dulled by fine shagreening and minute sparse punctures. Pronotum as in female. Mesoscutum and scutellum with crowded punctures and fine shagreening dulling surfaces. Propodeum sculptured as in female; mesepisterna with distinct punctures and shagreening dulling surface. Metasomal terga 2–5 sculptured as in female terga 2–4, surfaces shiny. Tergum 7 with pseudopygidial area absent or extremely narrow and hidden by hairs. Sterna 2–5 with basal areas punctate, apical areas impunctate, dulled by coarse shagreening. Terminalia as in *decolorata* as described below.

**Vestiture.** Pale yellowish to ochraceous except reddish brown on vertex and along inner margins compound eyes. Clypeus weakly bearded; hind basitarsus with long sparse

hairs, along anterior margin moderately long; metasomal tergum 2–4 with basal area hairs short, mostly shorter by half than those of tergum 1 and distinctly shorter than hairs of apical areas, erect; sterna 2–5 with subapical fimbriae weak.

**Type Material.** The female holotype (CAS No. 11,394) of *Andrena* (*O.*) *camissoniae* was collected from 28 mi. NW of New Cuyama, Santa Barbara Co., California, June 8, 1963, at flowers of *Camissonia campestris* (as *Oenothera dentata*) by G.I. Stage.

**Distribution.** *Andrena* (*O.*) *camissoniae* is known from only a few localities in southern California (Fig. 6). It has been collected March 30 to June 8 from the localities listed below.

CALIFORNIA. FRESNO CO.: Coalinga (7 mi. W). MONTEREY CO.: Arroyo Seco Camp (near Greenfield). SANTA BARBARA CO.: New Cuyama (28 mi. NW).

**Floral Records.** *Camissonia campestris*.

*Andrena* (*Onagrandroidrena*) *decolorata*, new species.

*Andrena decolorata* is a second large pale species similar in color of the vestiture in both sexes to *A. camissoniae*. Like the previous three species *decolorata* has the pronotum with well-formed humeral angles and lateral ridges, the male mandibles decussate and the male genal area twice as broad as the eye in profile. This species can be told from *camissoniae* in both sexes by the propodeum being more declivous with a distinct dorsal surface lacking, terga 2–4 with basal areas having longer hairs (especially tergum 2), and the propodeum and mesepisterna being more finely sculptured as described below.

**FEMALE: Measurements and Ratios.** N = 7; length, 12–14 mm; width, 3.5–4.0 mm; WL, M =  $4.36 \pm 0.231$  mm; FL/FW, M =  $1.05 \pm 0.007$ ; FOVL/FOVW, M =  $3.14 \pm 0.076$ .

**Integumental Color.** Black except as follows: mandible with apical half rufescent; flagellum bright orange to red below; wing membranes hyaline, colorless or slightly infumate, veins red to reddish brown; metasomal terga with apical areas somewhat translucent, rufescent; tibial spurs yellow.

**Structure.** Antennal scape as long as first four flagellar segments or almost so; flagellar segment 1 about as long as segments 2 plus 3 or slightly shorter, segment 2 slightly shorter than 3; segments 4–10 longer than broad. Eyes each about three and one-half times as long as broad, inner margins parallel. Mandibles long, moderately decussate, with distinct subapical tooth. Malar space linear, minimum length equal about one-tenth basal mandibular width. Galea pointed, broader near base, outer margin gently concave, weakly punctate, dulled by regular fine tessellation. Maxillary palpus long, extending beyond tip of galea by last two segments or more, segmental ratio about as 1.0:1.0:0.9:0.7:0.7:0.8. Labial palpus with long curved first segment, segmental ratio about as 1.0:0.5:0.4:0.5. Labral process (Fig. 23) large, apical part longer than broad, sides concave, weakly emarginate apically; labrum apical to process not sulcate, shiny. Clypeus shiny, with abundant small punctures separated by half puncture width or less except in impunctate midline, shagreened near base. Supraclypeal area dulled by fine shagreening and minute punctures. Face above antennal fossae longitudinally rugulate and punctate, surface moderately dulled, fossae separated from lateral ocellus by about half an ocellar diameter. Vertex above lateral ocellus short, equal to about half an ocellar diameter or slightly more. Genal area in profile distinctly broader than eye (about as 7:6), surface dulled by reticular shagreening, punctures minute, sparse.

Pronotum with humeral angles and lateral ridge, ridge not sharp or lamellate, surface dull, shagreened. Mesocutum with minute round punctures separated by half to one puncture width, surface shagreened, dull. Scutellum similar but shagreening weaker. Metanotum densely punctate and shagreened. Propodeum with dorsal surface lacking, declivous from anterior margin; dorsal enclosure with weak rugulae but median rugula usually complete,

shagreened; surface outside of enclosure with minute punctures separated by several puncture widths, surface dulled by shagreening. Mesepisterna sculptured similar to propodeum outside of dorsal enclosure. Fore wing with pterostigma narrow, long; vein first m-cu meets second submarginal cell beyond middle (usually near outer fourth).

Metasomal tergum 1 with apical area about as long as basal area, basal area punctures small, separated by one to three or four puncture widths, apical area punctate in basal half or more, punctures minute, surfaces dulled by coarse shagreening. Terga 2–3 with apical areas about as long as half of basal area, basal area punctures separated mostly by about 2 puncture widths or less, apical area punctate in basal half or slightly more, surfaces shiny, shagreening weak or absent. Pygidial plate with rounded apex, longer than broad at base, internal raised triangle weak, surface finely tessellate, dull. Sterna with basal areas distinctly punctate, apical areas impunctate, surfaces moderately shiny to dull, coarsely shagreened sternum 2 with long hairs of basal area similar to those of sternum 1.

**Vestiture.** Almost entirely pale, pale ochraceous to ochraceous, darker above, head with reddish brown hairs on vertex, along inner margins of eyes and along outer margins of eyes at least above; facial fovea with tomentum reddish brown in upper half, pale ochraceous below. Propodeum with lateral corbícula not distinctly formed, internal hairs long, plumose; hind tibiae with scopal hairs long, simple, sparse; trochanteral flocculus complete, weak; metasomal terga without fasciae.

**MALE: Measurements and Ratios.** N = 16; length, 11.5–13.0 mm; width, 2.5–3.5 mm; WL, M =  $3.79 \pm 0.291$  mm; FL/FW, M =  $1.02 \pm 0.006$ ; FS1/FS2, M =  $1.25 \pm 0.028$ .

**Integumental Color.** Black except as follows: mandible with apical half or less rufescent; antennal flagellum reddish brown to brown below; wing membranes hyaline, colorless to slightly yellowed, veins red to reddish brown; metasomal terga with apical areas translucent, red to reddish brown; tibial spurs rufescent to testaceous.

**Structure.** Antenna moderately long, in repose reaches about midscutellum; scape length equals first two and one-third flagellar segments; flagellar segment 1 distinctly longer than segment 2 and about equal to segment 3, all segments longer than broad. Eyes each almost three and one-half times as long as broad in facial view, inner margins diverge slightly towards vertex. Mandibles decussate, subapical tooth present, small (Fig. 24). Galea as in female. Maxillary palpus as in female, segmental ratio not visible. Labial palpus as in female, segmental ratio about as 1.0:0.6:0.4:0.6. Labral process large, about as long as broad, bidentate apically; labrum apical to process without sulcus or cristae. Clypeus sculptured as in female but lacking median impunctate line and punctures larger, surface shiny throughout. Supraclypeal area and face above antennal fossae as in female. Vertex above lateral ocellus equals to half an ocellar diameter or more but less than one diameter (allotype almost one). Genal area broad, with rounded knob about opposite midpoint of compound eye, surface sculptured as in female.

Pronotum with humeral angle and lateral ridge as in female. Mesoscutum, scutellum, metanotum sculptured as in female. Propodeum as in female but enclosure with slightly more rugulae near base (Fig. 25); mesepisternum with small round punctures separated by half to one and one-half puncture widths, interpunctural spaces finely tessellate. Wing venation as in female.

Metasomal tergum 1 sculptured as in female but somewhat shinier. Terga 2–5 sculptured as in female terga 1–4 but basal area punctures slightly denser, separated mostly by one to two puncture widths, apical area punctures restricted to basal half, surfaces shiny. Tergum 7 with extremely narrow pseudopygidial area, almost parallel-sided. Sterna 2–5 sculptured as in female but basal area punctures sparser and shagreening usually coarser. Genital capsule as shown (Fig. 26). Sterna 7 and 8 similar to *rubrotincta* but sternum 7 with apical lobes narrower and sternum 8 more distinctly capitate (Figs. 63 and 64).



**Vestiture.** Pale ochraceous to ochraceous except as follows: brown to reddish brown across vertex, along inner margins eyes and in upper half along outer eye margins. Terga without apical pale fasciae; sterna with subapical fasciae present but weak, hairs relatively short; hind tibiae with hairs sparse, long, along anterior and posterior margins some hairs almost as long as dorsal femoral hairs; metasomal tergum 2 with basal area with long hairs longer than those of apical area and similar to those of tergum 1; terga 3 and 4 with basal hair hairs decreasing in length.

**Type Material.** The holotype female of *Andrena* (*Onagrandroidrena*) *decolorata* was collected 3 miles NE of Moreno, Riverside Co., California, April 5, 1963, by W.A. Steffan. The allotype male was collected 4 miles E of Elsinore, Riverside Co., in Railroad Canyon, April 14, 1965, by D. Veirs (Fig. 6). The holotype and allotype will be deposited in the collection of the California Academy of Sciences. Six female and 16 male paratypes (UCB, UCR, UCD, LACM, INHS) are as follows:

CALIFORNIA. RIVERSIDE CO.: Hemet: 1 female, April 26, 1961, from *Cryptantha* sp., Ewart and Browner; Millard Canyon: 1 female, April 18, 1968, from *Madia* (as *Layia*) *exigua*, P.H. Timberlake. SAN BERNARDINO CO.: Seeley Flats, San Bernardino Mts.: 1 female, July 3, 1917, H. Klotz; 1 female, July 10, 1917, R. May. SAN DIEGO CO.: Descanso-Alpine Site: 1 male, March 17, 1972, from *Cryptantha barbigera*, A.R. Moldenke; 1 male, March 17, 1972, from *Mirabilis californica* (as *laevis*), A.R. Moldenke; 7 males, April 5, 1972, from *Cryptantha intermedia*, A.R. Moldenke; 1 male April 5, 1972, from *Mirabilis californica* (as *laevis*), A.R. Moldenke; 1 female, 1 male, April 5, 1972, from *Salvia apiana*, A.R. Moldenke; 1 male, April 19, 1972, from *Cryptantha* sp., A.R. Moldenke; 1 male, April 25, 1972, from *Camissonia californica* (as *leptocarpa*), A.R. Moldenke; Lakeside (2 mi. NE), March 13, 1968, J. Powell; Newton (8 mi. NW): 2 males, April 14, 1934, from *Cryptantha intermedia*, P.H. Timberlake. MEXICO. BAJA CALIFORNIA DEL NORTE: La Zapopita, Valle de Trinidad: 1 female, April 9–14, 1961, F.S. Truxal.

**Floral Records.** Presumably this species is an oligolege of the genus *Camissonia*. It has been collected from flowers of plants listed below.

*Camissonia californica* (as *leptocarpa*), *Cryptantha* sp., *C. barbigera*, *C. intermedia*, *Madia* (as *Layia*) *exigua*, *Mirabilis californica* (as *laevis*), *Salvia apiana*.

INDEX OF SPECIES NAMES

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<i>furva</i> Linsley and MacSwain .....	11, 15, <b>24</b> , 25.
<i>grundeli</i> Linsley and MacSwain .....	<b>18</b> .
<i>knowltoni</i> Linsley and MacSwain .....	<b>15</b> .
<i>linsleyana</i> Thorp .....	12, 13, 17, <b>17</b> .
<i>linsleyi</i> Timberlake .....	11, 13, 17, <b>36</b> .
<i>micranthophila</i> Cockerell .....	<b>15</b> .
<i>mojavensis</i> Linley and MacSwain .....	10, 13, <b>46</b> , 48.
<i>nevadae</i> Linsley and MacSwain .....	12, 17, <b>40</b> .
<i>oenotherae</i> Timberlake .....	12, 14, <b>26</b> , 31.
<i>omninigra</i> Viereck .....	11, 14, <b>18</b> , 21.
<i>oraria</i> Linsley and MacSwain .....	<b>26</b> .
<i>Onagrandrena</i> .....	<b>2</b> .
<i>raveni</i> Linsley and MacSwain .....	11, 13, 25, <b>40</b> .
<i>rozeni</i> Linsley and MacSwain .....	12, 14, 21, <b>34</b> .
<i>rubrotincta</i> Linsley .....	10, 13, <b>44</b> , 48.
<i>stagei</i> Linsley and MacSwain .....	12, 31, <b>32</b> .
<i>subhyalina</i> Linsley and MacSwain .....	<b>26</b> .
<i>thorpi</i> Linsley and MacSwain .....	<b>33</b> .
<i>vanduzeei</i> Linsley .....	14, 25, <b>43</b> .
<i>vespertina</i> Linsley and MacSwain .....	12, 14, <b>29</b> , 31.

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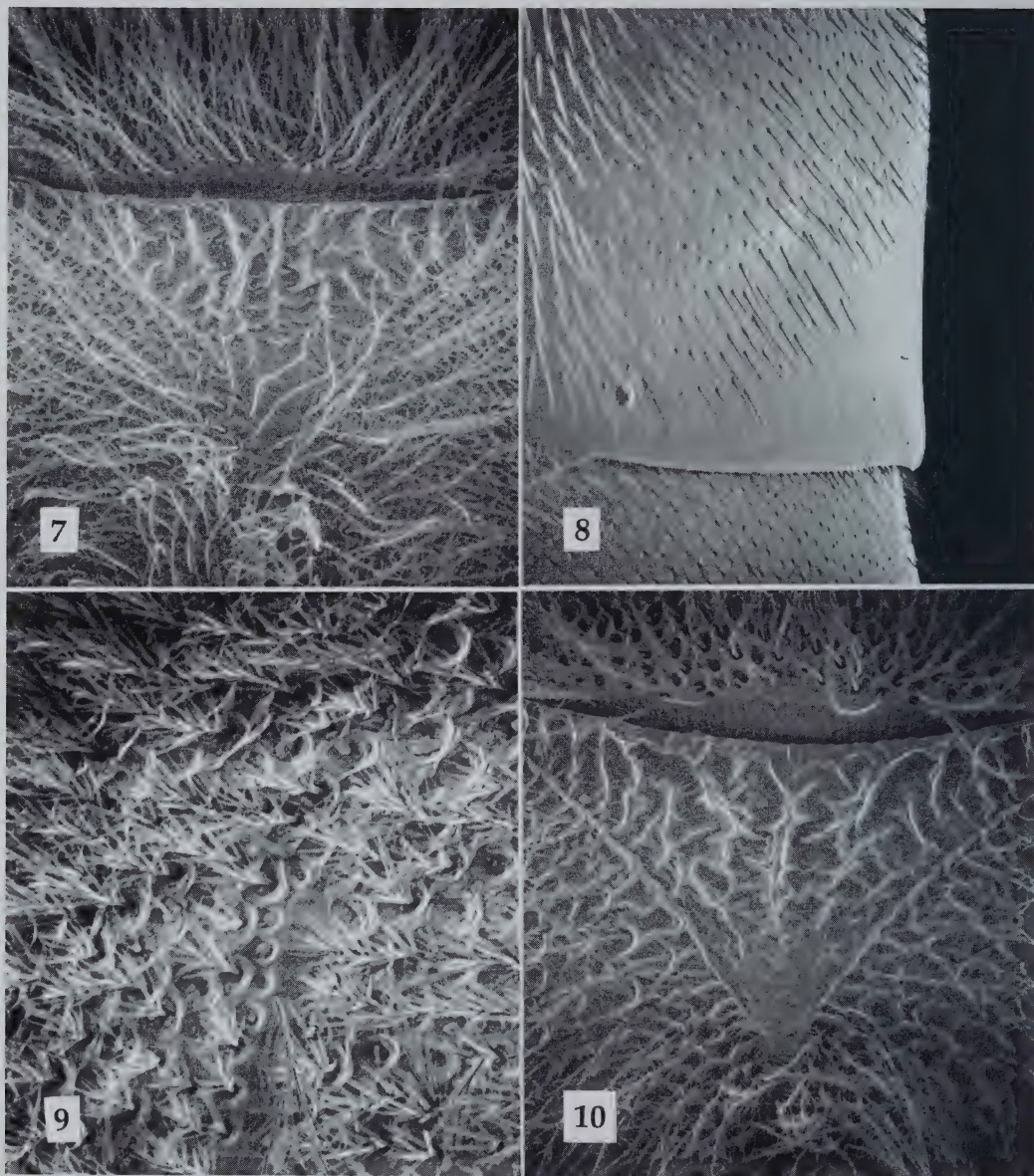
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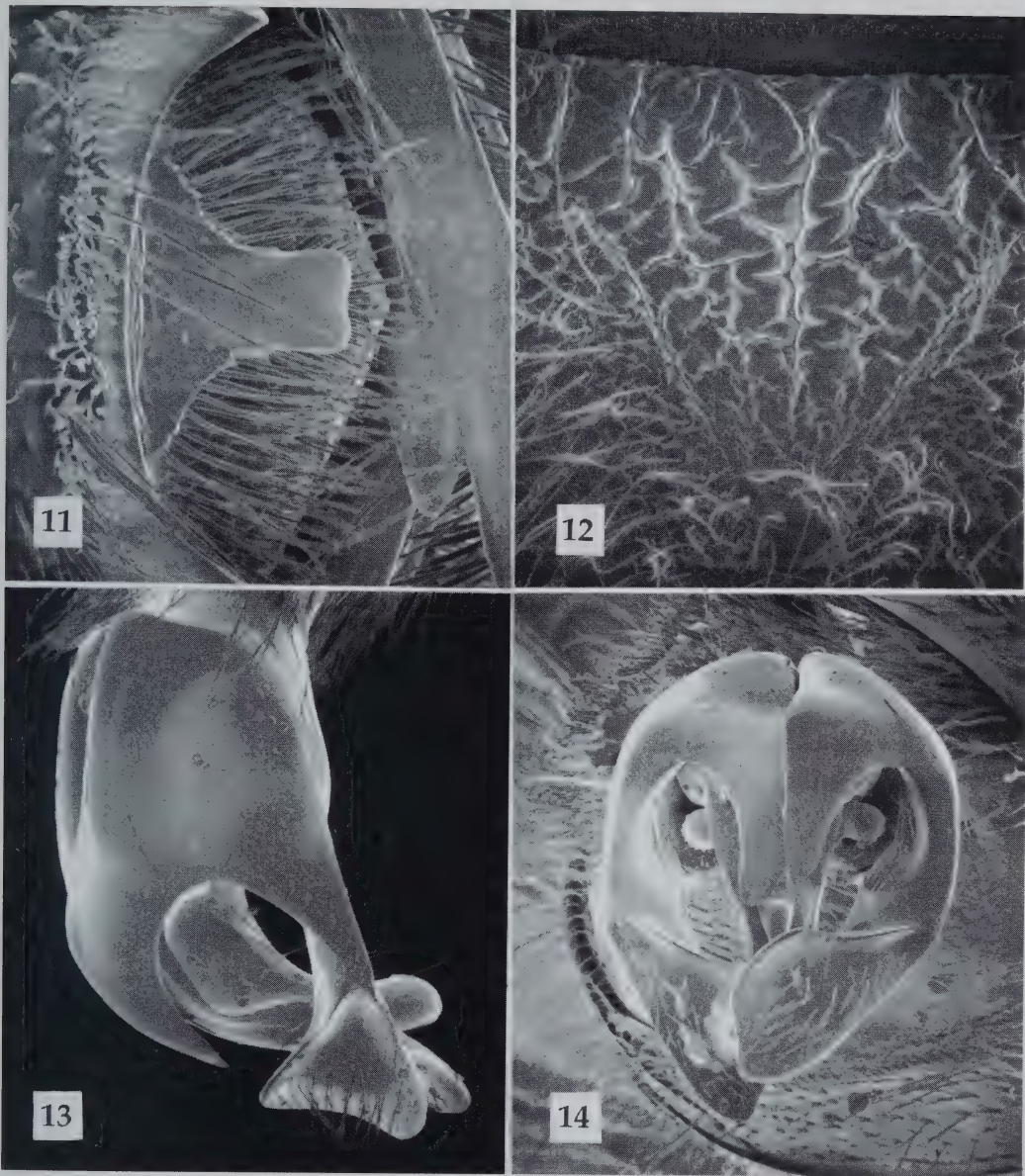
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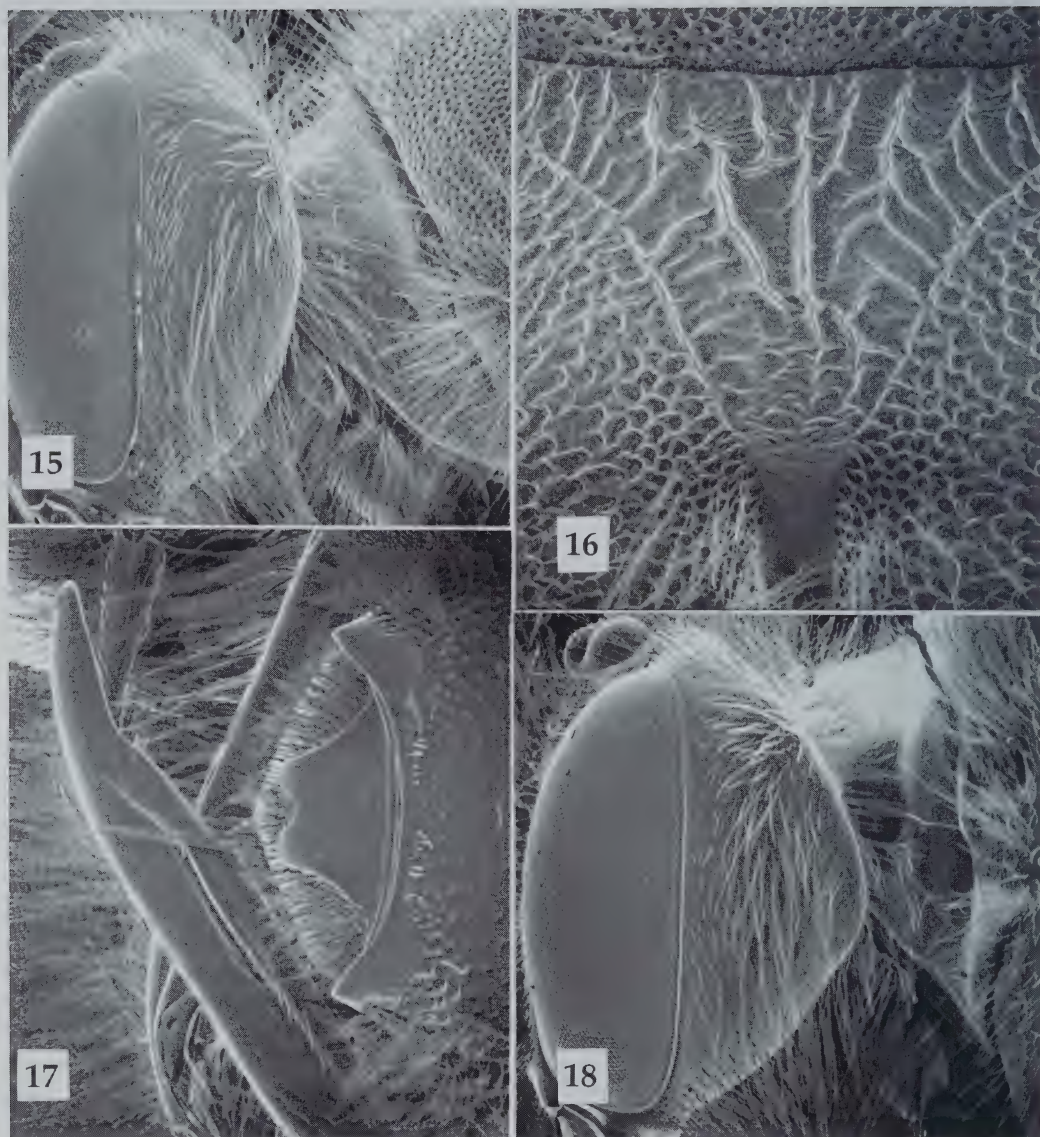


Figs. 7-10. *Andrena onagrae* Cockerell: 7—male propodeal dorsal area, X70. *Andrena flandersi* Timberlake: 8— male, profile view, tergum two, X1000. *Andrena furva* Linsley and MacSwain: 9—female, mesoscutum showing left parapsidal line, X200. *Andrena oenotherae* Timberlake: 10— male, propodeal dorsal area, X100.



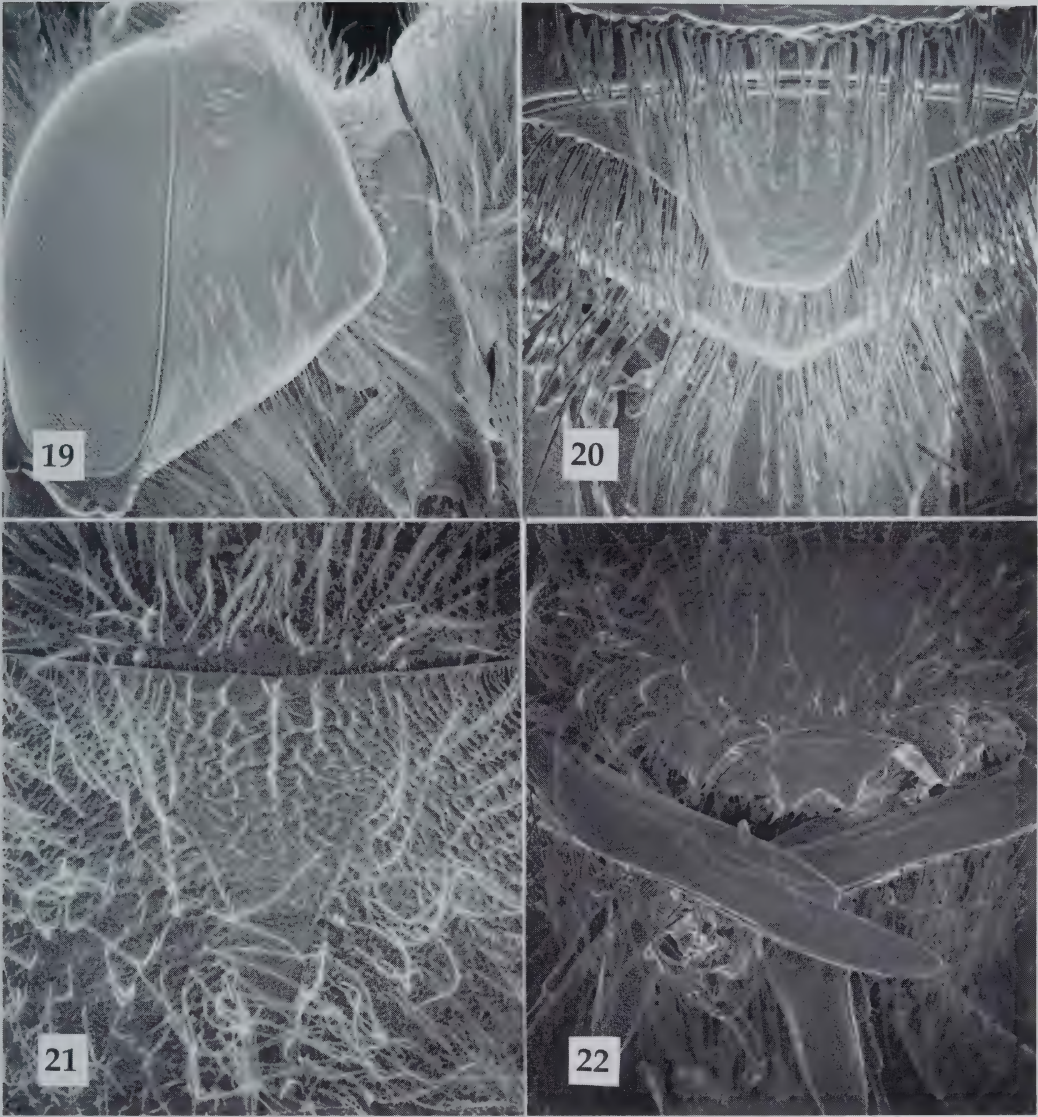


Figs. 11–14. *Andrena oenotherae* Timberlake: 11—female labral process, X100. 12—female propodeal dorsal area, X100. 13—male genital capsule, lateral view, X70. 14—male genital capsule, end view, X40.



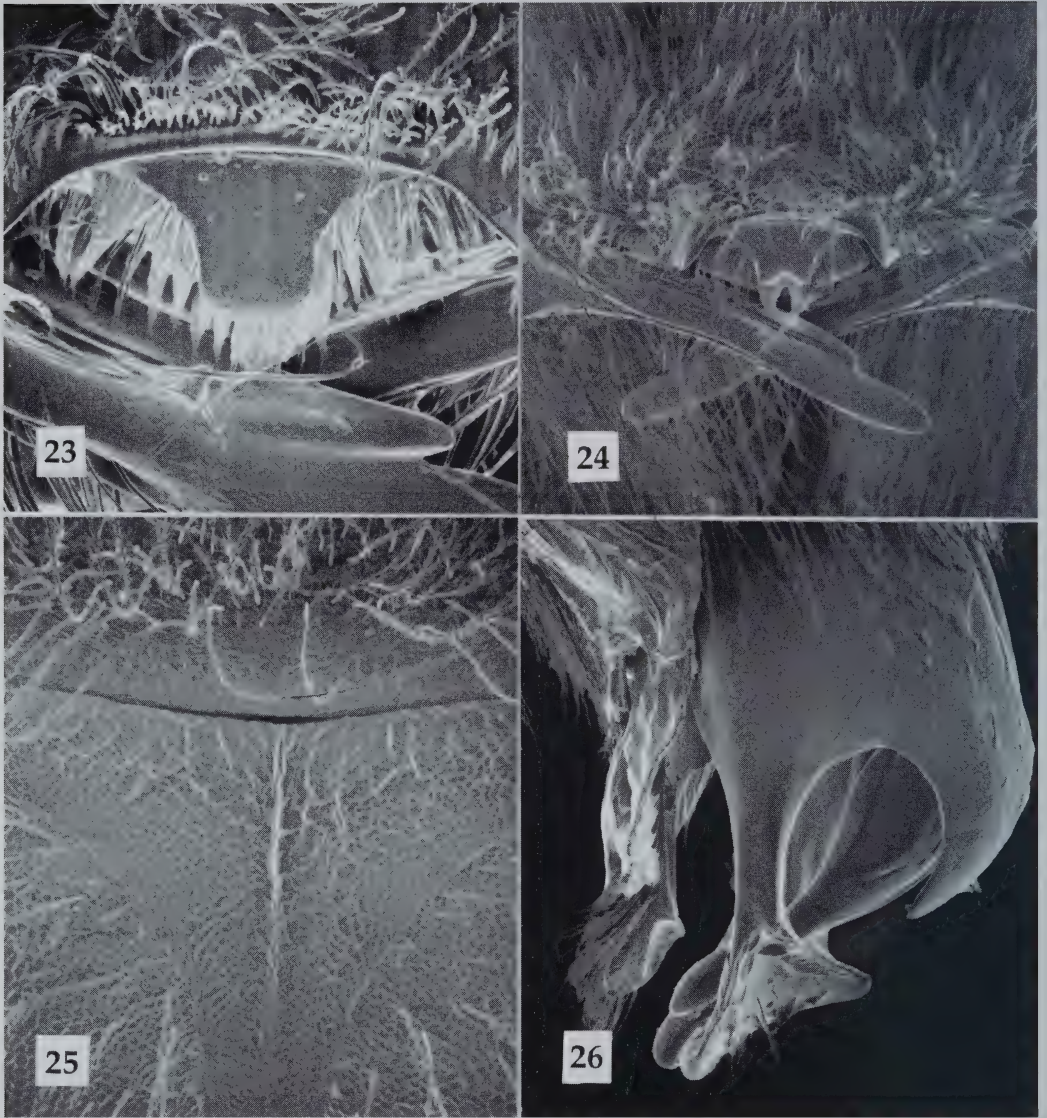
Figs. 15–18. *Andrena vespertina* Linsley and MacSwain: 15—female, lateral view of head and prothorax, X30, note lack of pronotal angle or lateral ridge. *Andrena nevadae* Linsley and MacSwain: 16—female propodeal dorsal area, X70. *Andrena rubrotincta* Linsley: 17—male labral process and simple mandible, X70. 18—female head and pronotum, lateral view, X30, note pronotal angle and lateral dorsoventral ridge.



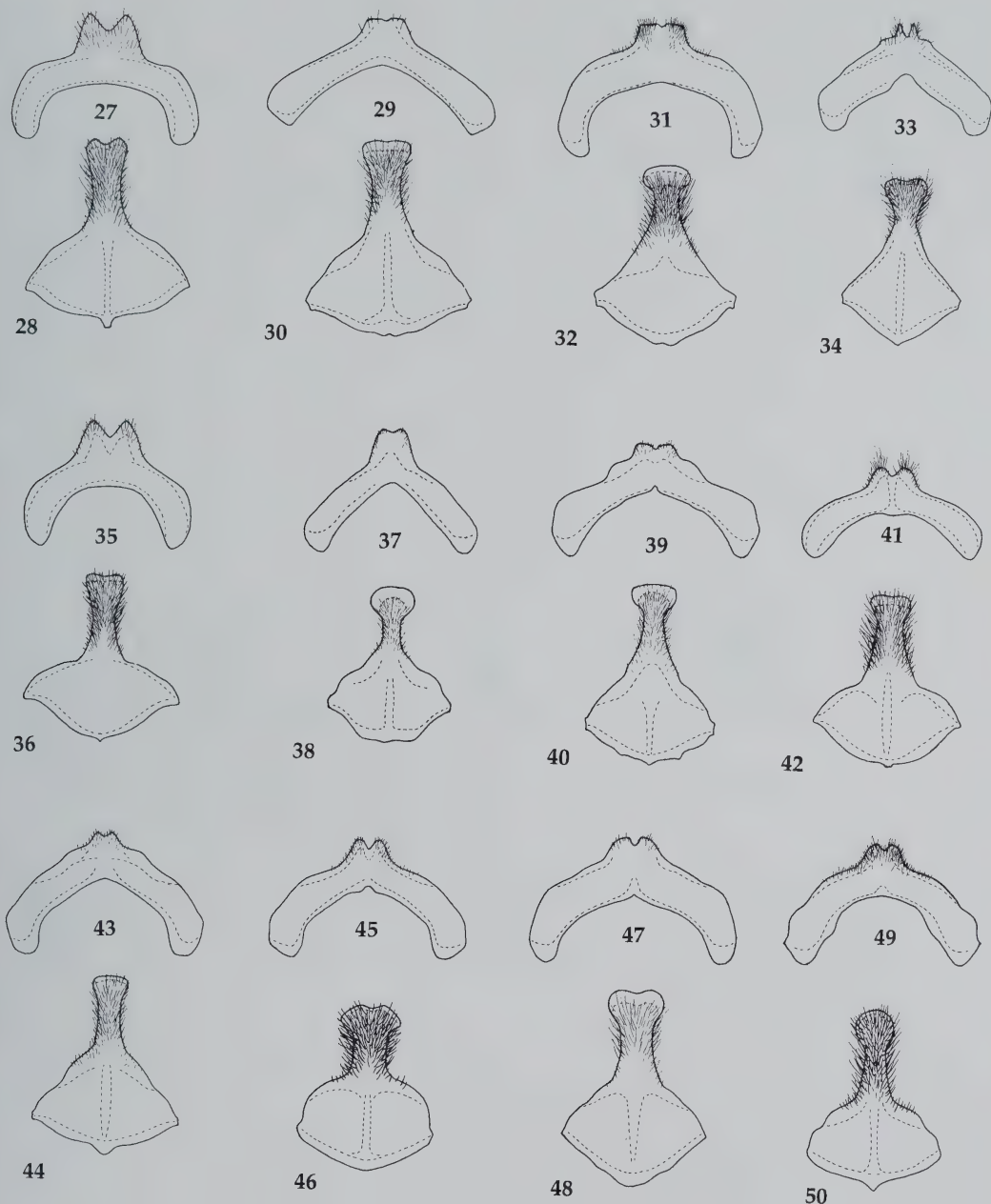


Figs. 19–22. *Andrena rubrotincta* Linsley: 19—male head (lateral view) and pronotum, X40, note pronotal angle and prominent genal posterior angle; 20—female labral process. *Andrena camissoniae* Linsley and MacSwain: 21—female propodeal dorsal area, X70; 22— male labral process and mandible, X50.

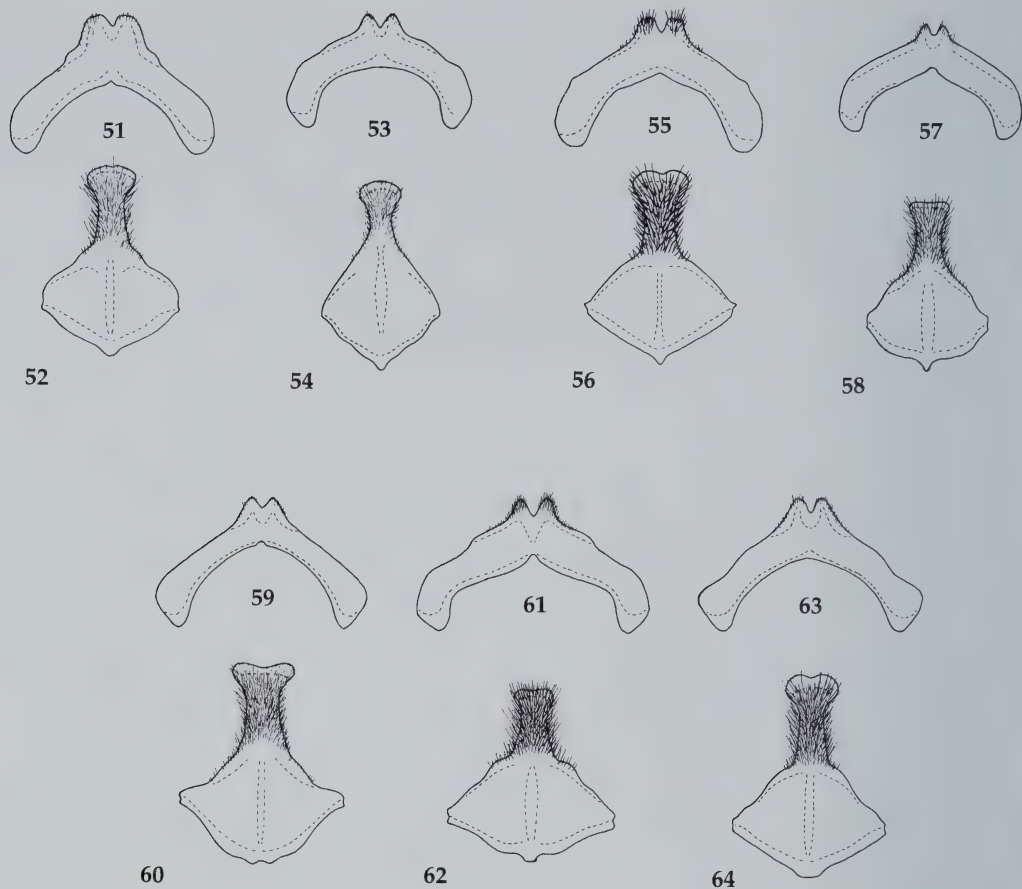




Figs. 23–26. *Andrena camissoniae* Linsley and MacSwain: 23—female labral process and mandible, X100. *Andrena decolorata* LaBerge and Thorp: 24—male labral process and mandible, X 40; 25—male propodeal dorsal area, X100; 26—male genital capsule, lateral view, X70.



Figs. 27–50. Sterna 7 and 8 of males of *Andrena* (*Onagrandrena*): 27–28—*A. anograe* Cockerell. 29–30—*A. linsleyana* Thorp. 31–32—*A. omninigra* Viereck. 33–34—*A. bernardina* Linsley. 35–36—*A. flandersi* Timberlake. 37–38—*A. furva* Linsley and MacSwain. 39–40—*A. blaisdelli* Cockerell. 41–42—*A. oenotherae* Timberlake. 43–44—*A. boronensis* Linsley and MacSwain. 45–46—*A. chylismiae* Linsley and MacSwain. 47–48—*A. vespertina* Linsley and MacSwain. 49–50—*A. rozeni* Linsley and MacSwain.



Figs. 51-64. Sterna 7 and 8 of males of *Andrena* (*Onagrandrena*): 51-52—*A. linsleyi* Timberlake. 53-54—*A. deserticola* Timberlake. 55-56—*A. raveni* Linsley and MacSwain. 57-58—*A. vanduzeei* Linsley. 59-60—*A. rubrotincta* Linsley. 61-62—*A. mojavenensis* Linsley and MacSwain. 63-64—*A. decolorata* LaBerge and Thorp.



APPENDIX 1. *Onagrandrena* phylogeny data matrix for Figure 1 based on characters listed in Table 1.

[	0	10	20	]
MATRIX				
decolorata	00010000000000111000000			
camissoniae	00000000000000101000000			
mojavensis	00100000010001010000000			
rubrotincta	00100000010001010100000			
bernardina	1110110010110100001001			
omninigra	1110111010010000001001			
flandersi	1110100010011000001011			
furva	1110101010110000100011			
raveni	1110000110010100001001			
linsleyi	1110000001000111000001			
vanduzeei	1110001110010000010001			
blaisdelli	1110000010110101100001			
rozeni	1110000010000000001001			
stagei	11100010100101011---			
boronensis	1110001010010000101001			
vespertina	1110001010010000101001			
oenotherae	1110001010010000101001			
chylismiae	1110001010010100101101			
nevadae	11100000100001001---			
deserticola	1110000010000000100001			
linsleyana	1110000010010011001101			
anograe	1110000010010000001001			
ancestor	0000000000000000000000			



ILLINOIS  
NATURAL  
HISTORY  
SURVEY

A Revision of the Bees of the Genus  
*Andrena* of the Western Hemisphere  
Part XV. Subgenus *Hesperandrena*

Robbin W. Thorp and Wallace E. LaBerge

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## ABSTRACT

This work reports on a study of 1,200 specimens segregated into 9 species, 4 of which are new to science. One name is relegated to synonymy. The relationships within the subgenus and with other subgenera of *Andrena* are briefly discussed.

## INTRODUCTION

The subgenus *Hesperandrena* was recognized and described by Timberlake in Lanham 1949 (p. 208) to include two previously described species, *Andrena escondida* Cockerell and *Andrena baeriae* Timberlake. These two species have in common a propodeum which Timberlake described as having the dorsal surface, "... broad, gently curved and inclined from base to apex, without definite truncation, the lateral margins distinctly carinate and convexly arcuate." This is the main character separating this subgenus (Fig. 4) from other subgenera of *Andrena* except that in the males of *Hesperandrena* the lateral margins of the propodeum are not carinate. Other characters are given in the description of the subgenus below. The species of this subgenus are very similar to one another and difficult to tell apart. The species are known only from California and Baja California.

The reader is referred to earlier sections of this revision (LaBerge 1967, 1969, 1971, 1973, 1977, 1980, 1986, 1987, 1989; LaBerge and Bouseman 1970, 1987; LaBerge and Ribble 1972, 1975; Bouseman and LaBerge 1979; Thorp 1969; Donovan 1977) for details of morphology and a more complete bibliography on the genus *Andrena*. No new terms have been introduced and the bibliography presented here includes only references cited. Published locality and floral records are included in the sections at the end of each species account. Institutions with type material are listed with contractions as follows:

AMNH—American Museum of Natural History, New York City

CAS—California Academy of Science, San Francisco

INHS—Illinois Natural History Survey, Champaign

LACM—Los Angeles County Museum (of Natural History), Los Angeles

PANS—Philadelphia Academy Natural Sciences

USNM—United States National Museum (of Natural History), Washington, D.C.

UCB—University of California at Berkeley (Entomology Collection)

UCD—University of California at Davis (Entomology Collection)

UCR—University of California at Riverside (Entomology Collection)

UKL—University of Kansas, Lawrence

USU—Utah State University, Logan

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### Subgenus *HESPERANDRENA* Linsley and MacSwain

*Hesperandrena* Timberlake, 1949, in Lanham, 1949, Univ. California Pub. Ent., 8:208; LaBerge, 1964, Univ. Nebraska St. Mus. Bull., 4:301; 1986, Trans.American Ent. Soc., 111:443, 447, 452.

Bees of the subgenus *Hesperandrena* are small to medium with short malar spaces, short vertices (never taller than one ocellar diameter and mostly shorter), and genal areas of moderate width. Both sexes have relatively weak sculpturing, propodeal dorsal areas smooth with small, sparse punctures, and the terga with weak but distinct pale apical fasciae. The females have the propodeal corbícula developed but with internal hairs and scopal hairs that are moderate in length and weakly branched or simple. The males may or may not have subapical sternal fimbriae. We believe the flattened branchless hairs on sternum 7 to be a unique character found only in males of *Hesperandrena*.

**Common Characters.** Small to medium-sized bees; facial quadrangle quadrate to slightly wider than long; eyes with inner margins parallel to converging slightly towards mandibles; vertex above lateral ocellus usually equals less than one ocellar diameter; genal area as broad as eye in profile or slightly broader; galea broad with concave lateral margin, exceeded by one maxillary palpal segment or slightly more or less; labral process simple or bidentate, often shallowly emarginate; cheeks moderately broad, rounded behind.

**Female.** Facial fovea large, shallow; subgenal coronet present. Propodeal corbícula present, with well formed, long, dorsal hairs, usually with internal plumose hairs. Trochanteral flocculus present but usually sparse. Tibial scopal hairs moderately long, usually weakly branched.

**Male.** Antennae short, female-like, first segment usually longer than second. Sterna with subapical fimbriae; sternum 7 with apical lobe deeply emarginate; sternum 8 with area basal to expanded apex with flat, broad hairs with attenuate apices (Fig. 9).

### PHYLOGENY

The phylogeny of the subgenus *Hesperandrena* is not clearly understood at present and additional work is obviously needed. We assume that the subgenus is closely related to the subgenera *Larandrena*, *Andrena s. str.*, *Opandrena*, *Ptilandrena*, and *Leucandrena*. All of these subgenera have species occurring today on the west coast where the *Hesperandrena* probably originated and all share in the modified pronotum with lateral angles and ridges usually being present. We believe the *Hesperandrena* to be especially similar to, and perhaps most closely related to the *Larandrena* and *Ptilandrena*.



## BIOLOGY

Females of *Hesperandrena* appear to be oligolectic, most on Asteraceae but one species, *A. pulvereae*, on flowers of Limnanthaceae. Because most of the *Hesperandrena* live in association with vernal pool ecosystems in California, the *Hesperandrena* are becoming recognized as an important group in conservation planning and mitigation issues. These species provide an important ecological service in pollination of showy flowers in vernal pool communities.

**Distribution and Abundance.** *Hesperandrena* is predominantly a California subgenus with one species reaching northern Baja California in Mexico (Thorp and Leong, 1998). Most are abundant when the showy displays of their pollen plants, *Lasthenia* (goldfields) or *Limnanthes* (meadowfoam), bloom in early spring.

**Overwintering, Emergence, and Flight Season.** Species of *Hesperandrena* have annual life cycles and emerge in early spring in association with bloom of their pollen plants (Thorp, 1990). They fly from early March into early July but are most abundant in March and April. Circumstantial evidence for the ability to delay emergence for a year during severe drought conditions is presented for *A. pulvereae* Viereck (as *limnanthis* Timberlake) by Thorp (1990).

**Male Behavior.** Most species of the genus exhibit proterandry, i.e., males emerge before females. Males often cruise the pollen host plants of females, but some also cruise clustered nests.

**Nest-sites, Architecture, and Construction.** The nests of *Hesperandrena* are shallow, 7.5 to 10.2 cm deep, especially in vernal pool ecosystems where soil is shallow and the water table high. The burrows are typically L-shaped with a single brood cell at the end of each short lateral. There is usually more than one lateral per burrow, with each lateral filled after the egg is laid and the cell capped. Fill presumably comes from the succeeding lateral. Details of brood cells, pollen mass formation, cell cap, egg, and early larval position are figured in Thorp (1990). Brood cells are lined with a waxlike material. Pollen is deposited in the bottom of the cell and worked into a spherical mass with the addition of nectar. An egg is then deposited atop the mass. The larva ecloses from the egg, feeds, and progresses through its development during the spring. By summer it has reached the post-defecating stage and remains thus until autumn. During the autumn the larva pupates and transforms into an adult, but remains in the brood cell over the winter. The adult emerges in spring in synchrony with bloom of its pollen-host plant.

**Flower Relationships.** Females are mostly oligolectic on Asteraceae, especially *Lasthenia* (Thorp and Leong, 1995). One species, *A. pulvereae* (as *limnanthis*), is an oligolectic of *Limnanthes* (Limnanthaceae) (Thorp and Leong, 1995). Using three colors of pan-traps to sample bees in patches of the white-flowered *Limnanthes douglasii* R. Br. var. *rosea* (Benth.) C. Mason, Leong and Thorp (1999) found that females of *A. pulvereae* (as *limnanthis*) were most frequently trapped about equally in white and blue pans, while males were trapped predominantly in white pans. Yellow pans produced significantly lower captures of both sexes of this species. Other *Andrena*, especially those that are oligolectic of yellow flowers were most frequently trapped in the yellow pans. The females of *A. pulvereae* were the most common bees found in patches of *Limnanthes* by Leong and Thorp (1990). The foraging patterns of *Hesperandrena*, especially females foraging for pollen, may influence genetic structure of pollen-host populations through near-neighbor, bee-mediated pollen flow (Thorp, 1999).

**Pollen Competition.** Two or more species of *Hesperandrena* often occur together (Thorp and Leong, 1998). Because they forage for pollen on different hosts, no resource overlap occurs between *A. pulvereae* (as *limnanthis*) and other species of *Hesperandrena*. Nevertheless, pollen resources are often shared by multiple species that are sympatric and oligolectic on *Lasthenia*.

**Parasites, Predators, and Associates.** **Strepsiptera: Stylopidae.** Female *Stylops* have been found between the abdominal terga of species of *Hesperandrena*. **Hymenoptera: Anthophoridae.** Females of cuckoo bees of the genus *Nomada* have been observed in the vicinity of nests of *Hesperandrena* (R. W. Thorp personal observation).

**Chromosome Number.** Chromosome numbers for *Hesperandrena* are unusually low for bees. Goodpasture (1974) found numbers of n=10 for *A. (Hesperanda) sp.* (probably *dissona* Thorp and LaBerge) and n=3 for *A. duboisi* Timberlake. He compared the karyotypes of the two *Hesperandrena* and found that the total genome length in *duboisi* was half that in *dissona*, the other species he studied.

**Role in Conservation.** Vernal pool ecosystems are threatened in California. The important role of pollen-specialist solitary bees, especially *Andrena (Hesperandrena)* and *A. (Diandrena)*, as pollinators of many of the characteristic showy flowers and the need to protect these bees to continue their ecological service contributions have been stressed by Thorp (1976, 1990) and Thorp and Leong (1995, 1998). Females of *Hesperandrena* species are oligoleges of sensitive plants: *A. pulverea* on *Limnanthes vinculans* Ornduff (federally and state listed as endangered), and *A. [species? (probably duboisi and dissona)]* on *Lasthenia conjugens* Greene (Thorp personal observation). Both plants are endemic to California and are placed on List 1B (plants rare, threatened, or endangered in California and elsewhere) by the California Native Plant Society (Skinner and Pavlik 1994). These bee species are likely to be important pollinators of their endangered plant hosts and therefore part of the critical habitat necessary for the reproduction and perpetuation of the plants.

KEY TO THE FEMALES OF  
HESPERANDRENA

- 1. Scopal hairs short, hind tibia broad, subcuneate; labral process usually about as long as basal width, no less than three-fourths as long as wide; tergal apical fasciae narrow, ..... *pulverea* Viereck  
Scopal hairs uniformly long, hind tibia not broadened; labral process much shorter than its basal width, often half or less as long as broad; tergal apical fasciae often broad ..... 2.
- 2(1). Dorsal thoracic hairs mostly short; facial fovea broad above, separated from lateral ocellus by half an ocellar diameter or slightly more or less ..... *laticinctis* Timberlake  
Dorsal thoracic hairs mostly long; facial fovea narrow above, separated from lateral ocellus by one ocellar diameter or slightly more..... 3.
- 3(2). Mesoscutum anteriorly, mesepisternum, face below ocelli, and abdomen with metallic greenish reflection ..... 4.  
Mesoscutum and usually abdomen and face black, without metallic reflections ..... 5.
- 4(3). Mesoscutum posteromedially shiny, tessellation weak or absent, punctures distinct; pronotum with humeral angle and ridge distinct; forewings narrowly clouded near tips ..... *leucomystax* n. sp.  
Mesoscutum posteromedially usually dull, tessellate, punctures shallow, indistinct; pronotum with distinct humeral angle and dorsolateral ridge indistinct, especially below; forewings not clouded apically ..... *duboisi* Timberlake
- 5(3). Metasomal terga 1–3 with basal areas moderately shiny, shagreening coarse, especially apically, but not completely dulling surface; clypeus with basal

- half or slightly more with distinct punctures, apical third to half coarsely or punctatorugose..... *eremophila* n. sp.
- Metasomal terga 1–3 with basal areas dull, shagreening fine and dense, surfaces dull; clypeus with basal three-fourths or more with punctures fine, sparse, scarcely visible, apical fourth or less more coarsely..... punctate ..... 6.
- 6(5). Facial fovea with tomentum largely dark brown; mesoscutum and scutellum with hairs golden to brown; pronotal angle and ridge present but weak ..... *compositarum* n. sp.
- Facial fovea with tomentum silvery; mesoscutum without brown hairs, white to pale ochraceous; pronotal angle and ridge present and distinct or absent ..... 7.
- 7(6). Pronotum with distinct humeral angle and dorsolateral ridge..... 8.
- Pronotum without humeral angle or ridge ..... *escondida* Cockerell
- 8(7). Mesoscutum tessellate, just mesad of parapsidal line punctures shallow, small, indistinct, obscured by dense fine tessellation, not at all shiny postero-medially; scutellum dulled by tessellation..... *baeriae* Timberlake
- Mesoscutum shinier, punctures distinct, not at all obscured by tessellation, often shiny and untessellate at least posteromedially; scutellum usually shiny to moderately so, tessellation weak or lacking at least medially..... *dissona* n. sp.

# KEY TO THE MALES OF *HESPERANDRENA*

1. Sterna 2–5 with subapical fimbriae of extremely short, moderately dense, white, plumose hairs ..... 2.
- Sterna 2–5 with subapical fimbriae of long straight hairs, long curled hairs, or without fimbriae ..... 3.
- 2(1). Pronotum with distinct lateral angles and ridges; clypeus with dense beard of long, plumose, white hairs hiding surface; scutellum shiny at least medially, mesoscutum often shiny posteromedially ..... *leucomystax* n. sp.
- Pronotum with pronotal angles weak, lateral ridges not extending below diagonal pronotal suture; clypeus with long, pale, plumose hairs, but hairs relatively sparse; scutellum and mesoscutum dulled by fine dense tessellation ..... *duboisii* Timberlake
- 3(1). Sterna 2–5 lacking subapical fimbriae ..... *pulverea* Viereck
- Sterna 2–5 with subapical fimbriae of long, straight or curled, pale hairs ..... 4.
- 4(2). Sterna 2–5 with subapical fimbriae of dense, long, white, straight, plumose hairs; pronotum without lateral angles or dorsolateral ridges ..... *escondida* Cockerell.
- Sterna 2–5 with subapical fimbriae of relatively sparse, extremely long, pale downwards curled hairs; pronotum often with lateral angles and ridges ..... 5.



- 5(4). Clypeus dark, without yellow or cream-colored macula ..... 6.  
 Clypeus entirely pale or with large mediobasal, yellow or cream-colored.....  
 macula ..... 7.
- 6(5). Pronotal lateral carina sharply defined, extending from humeral angle to .....  
 bottom of pronotum ..... *baeriae* Timberlake  
 Pronotum with lateral carina weakly defined, extends ventrad to diagonal  
 pronotal suture ..... *compositarum* n. sp.
- 7(5). Integument with metallic green reflections, especially on face and anterior  
 third of mesoscutum; terga 2 and 3 rarely with pale brown lateral patches  
 ..... *dissona* n. sp.  
 Integument black, without metallic green reflections; terga 2 and 3 often  
 with small, pale brown, lateral patches..... *lativentris* Timberlake

# SPECIES ACCOUNTS

## *Andrena escondida* Cockerell

*Andrena escondida* Cockerell, 1938, Ann. Mag. Nat. Hist., ser. 11, 2:146.

*Andrena (Hesperandrena) escondida*: Timberlake, 1949, in Lanham, California  
 Univ. Publ. Ent., 8:208; Timberlake, 1951, Proc. United States Nat. Mus.,  
 101:386 Rust, Menke and Miller, 1985, Entomology of the California Channel  
 Islands: Proc. 1st Symp., San Diego, California, Dec. 1981, p. 42.

This small species with black integument can be recognized in the female sex by the lack of pronotal humeral angles and dorsolateral ridges, the short labral process, and the relatively strongly punctate mesoscutum. The male of *escondida* has the clypeus black, lacks pronotal humeral angles, and has well-formed, sternal, subapical fimbriae of relatively long, dense, straight hair

**FEMALE: Measurements and Ratios.** N = 12; length, 8.0–9.5 mm; width, 2.0–2.5 mm; WL, M = 2.61±0.189 mm; FL/FW, M = 0.95±0.029; FOVL/FOVW, M = 2.60±0.157.

**Integumental Color.** Black except as follows: mandible with apical third rufescent; flagellum with last several segments reddened below; wing membranes hyaline, veins red to reddish brown; metasomal terga with apices narrowly hyaline, becoming darker towards base; tibial spurs yellow.

**Structure.** Antennal scape as long as first three and one-half flagellar segments or slightly more; flagellar segment 1 as long as segments 2 plus 3, which are equal in length; segments 5–7 about as long as broad. Eyes each about four times as long as broad, inner margins parallel. Mandibles short, overlapping when closed by one fourth or less of mandibular length; with subapical tooth. Malar space short, linear. Galea pointed, outer margin gently concave in apical half; surface dulled by fine tessellation. Maxillary palpus relatively short, when extended surpasses galea by about last segment, segmental ratio about as 0.7:1.0:0.9:0.6:0.5:0.6. Labial palpus normal, segmental ratio about as 1.0:0.6:0.3:0.5. Labral process short, entire, about three times as long as broad, not emarginate apically or only extremely shallowly so; shiny; labrum apical to process at least as long as process, flat, shagreened. Clypeus short, gently rounded from side to side, surface dull, tessellate with sparse, indistinct punctures, which become crowded and more distinct in narrow apical band. Supraclypeal area dull, coarsely tessellate. Face above antennal fossae

with fine longitudinal rugulae and shagreening. Facial fovea extends to just below line across lower margins of antennal fossae, three times as long as broad; separated from lateral ocellus by about one ocellar diameter. Vertex above lateral ocellus short, equals less than one ocellar diameter. Genal area in profile equals about one and one-third times width of eye, surface dull, shagreened. Pronotum without humeral angles or lateral ridges, surface dull, shagreened.

Mesoscutum dull, finely tessellate, with punctures medially separated mostly by two or more puncture widths, near parapsidal lines and in anterior fifth or more; dorsal enclosure of propodeum finely punctatorugose basally, outside of enclosure tessellate with scattered obscure punctures; basal sulcus almost parallel-sided, short; dorsoposterior surface separated from lateral surfaces by distinct carinae. Pleurae dull, finely tessellate, punctures absent or obscure.

Metasomal tergum 1 tessellate, somewhat more finely so in apical area, with minute obscure punctures not much larger than tesserae, separated by two to four puncture widths. Terga 2–4 similarly sculptured, tergum 5 more densely punctate. Pygidial plate U-shaped, raised rim, if present, extremely narrow. Sterna 2–5 with basal areas finely tessellate, slightly shiny, with distinct punctures separated by half to two puncture widths.

**Vestiture.** White to pale ochraceous except as follows: facial fovea with tomentum silvery white to entirely white in lower half and pale yellow to golden in upper half; terga 5 and 6 with mediobasal hairs dark ochraceous; inner surfaces of tarsi light yellow. Dorsal thoracic hairs long, mostly longer than width of flagellum. Tergum 2 with apical fascia of pale hairs interrupted medially by less than one-third width of tergum; terga 3 and 4 with complete apical pale fasciae. Tibial scopal hairs simple to weakly plumose; propodeal corbicula incomplete anteriorly with long internal hairs; trochanteral flocculus complete but relatively sparse.

**MALE: Measurements and Ratios.**  $N = 16$ ; length, 7–9 mm; width, 1.5–2.5 mm; WL,  $M = 2.30 \pm 0.633$  mm; FL/FW,  $M = 1.02 \pm 0.008$ ; FS1/FS2,  $M = 2.06 \pm 0.043$ .

**Integumental Color.** As in female except terga 2–5 with apical areas more broadly hyaline apically.

**Structure.** Antennae short, female-like; flagellar segment 1 twice as long as segment 2 or slightly longer, segment 2 usually slightly longer than 3, broader than long, segments 4–7 about as long as broad; scape length as in female. Eyes each almost four times as long as broad, inner margins diverging towards vertex. Mandibles apposite, short, with subapical tooth. Galeae as in female. Maxillary palpus as in female but ratio about as 0.7:1.0:0.6:0.6:0.5:0.6. Labial palpus as in female but ratio about as 1.0:0.5:0.4:0.5. Labral process short, more than twice as broad as long, apical margin gently concave, surface shiny; labrum apical to process about as long as process, finely shagreened. Clypeus sculptured as in female but punctures slightly more distinct and denser, separated mostly by one to two puncture widths. Supraclypeal area, face above antennal fossae, and vertex and genal area as in female.

Pronotum as in female. Thoracic sculpturing as in female except as follows: anterior fifth of mesoscutum with punctures sparse, mostly separated by two puncture widths; propodeum with dorsoposterior and lateral surfaces separated by weak carinae extending up from below to about half the length of propodeum.

Metasomal terga 1–6 sculptured as in female terga 1–5 but surfaces slightly shinier. Sterna as in female. Sterna 7 and 8 as in Figs. 20 and 21. Note that sternum 7 has apical lobes evenly rounded on external edges and median emargination narrow. Sternum 8 has apex not at all emarginate or extremely shallowly so, area of broad, flattened hairs covering half or more of neck.

**Vestiture.** Generally white to pale ochraceous but inner surfaces of tarsi pale yellow. Metasomal terga 2–5 with weak short apical pale fasciae, those on terga 2 and 3 interrupted

medially and often on tergum 4. Sterna 2–5 with distinct pale subapical fimbriae of long, almost straight, dense, plumose, white hairs.

**Type Material.** The holotype male of *escondida* (CAS 15,331) was collected at Rancho Escondido, Santa Catalina Island, Los Angeles Co., California, from flowers of *Encelia californica*, March 31, 1938, by W.P. Cockerell.

**Distribution.** *Andrena escondida* is known (Fig. 1) from Yolo County in central California south to San Diego County. It has been collected from March 2 through May 12, but chiefly in March and April. A total of 12 females and 16 males from localities listed below (including localities cited in the literature) were studied.

CALIFORNIA. ALAMEDA CO.: Midway. FRESNO CO.: Big Panoche Creek (Fresno-San Benito County line). KERN CO. LOS ANGELES CO.: Gorman (5 mi. S); Los Angeles; Santa Catalina Island. SAN DIEGO CO.: Escondido. SAN JOAQUIN CO.: Hospital Canyon; Tracy (6 mi. W). SANTA BARBARA CO.: Cachuma Canyon (2 mi. NW). SOLANO CO.: Dixon (8 and 9 mi. S); Putah Canyon. STANISLAUS CO.: Modesto. TULARE CO.: Visalia. YOLO CO.: Davis.

**Floral Records.** *Andrena escondida* should be considered as an oligolege of composites of the genus *Layia*. It has been collected from the plants listed below (including records in the literature).

*Brassica* sp., *Calchortus catalinae*, *Encelia californica*, *Lasthena chrysostoma*, *Layia* sp., *L. chrysanthemoides*, *Plagiobothrys* sp.

### *Andrena (Hesperandrena) pulverea* Viereck

*Andrena pulverea* Viereck, 1917, Proc. Acad. Nat. Sci. Philadelphia, 68:569–570.

*Andrena (Hesperandrena) limnanthis* Timberlake, 1951, Proc. United States Nat.

Mus., 101:387–388. **New synonymy.**

The female of *Andrena pulverea* is like that of *escondida* in lacking pronotal humeral angles and lateral ridges but can be recognized by the large labral process which is entire, about one and one-half times as broad as it is long, usually triangular with a low apical boss. The male of *pulverea* is like that of *escondida* in having a black clypeus but can be separated from that species by the presence of weak humeral angles, flagellar segment 3 being slightly longer than segment 2, rather than the inverse, and the lack of sternal subapical fimbriae.

**FEMALE: Measurements and Ratios.** N = 20; length, 9–10 mm; width, 2.0–2.5 mm; WL, M =  $2.68 \pm 0.125$  mm; FL/FW, M =  $0.94 \pm 0.005$ ; FOVL/FOVW, M =  $3.04 \pm 0.047$ .

**Integumental Color.** Black except as follows: mandible with apical fifth to almost half rufescent; flagellum below dark brown; wing membranes hyaline, slightly infumate, yellowed, veins reddish brown to dark brown; metasomal terga with apical areas often slightly reddened, narrowly hyaline apically; tibial spurs yellow.

**Structure.** Antennal scape as long as first four flagellar segments or slightly shorter; flagellar segment 1 slightly longer than segments 2 plus 3, segments 2 and 3 subequal, shorter than 4, segments 5–7 about as long as broad. Eyes each almost four and a half times as long as broad, inner margins parallel. Mandibles short, apposite, with subapical tooth. Malar space short, linear. Galea as in *escondida*. Maxillary palpus as in *escondida* but segmental ratio about as 0.7:1.0:0.8:0.7:0.6:0.6. Labial palpus normal, segmental ratio about as 1.0:0.5:0.5:0.6. Labral process large, entire, usually triangular with blunted apex and small apical boss, occasionally rounded with apical boss; labrum apical to process as in *escondida*. Clypeus as in *escondida* but punctures sparse and indistinct almost to apical margin. Supraclypeal area and face above antennal fossae as in *escondida*. Facial fovea as



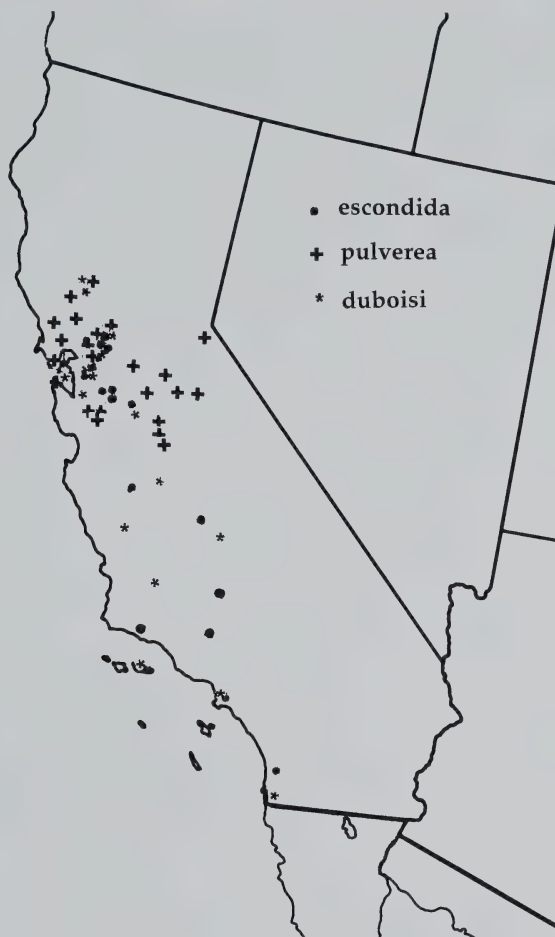


Fig. 1. Map showing the known distribution of *A. pulverea*, *A. escondida*, and *A. duboisi*.

in *escondida* but slightly longer. Vertex above lateral ocellus usually equals less than half an ocellar diameter. Genal area in profile as in *escondida*.

Pronotum as in *escondida*. Mesoscutum sculptured as in *escondida* but punctures sparse, obscure in anterior third and near parapsidal lines. Scutellum tessellate, punctures minute, widely separated. Propodeum as in *escondida* but dorsal enclosure not roughened basally. Pleurae as in *escondida*.

Metasomal terga sculptured as in *escondida*, punctures minute, essentially impunctate. Pygidial plate and sternal sculpturing as in *escondida*.

**Vestiture.** White to pale ochraceous except as follows: facial fovea with tomentum brown to golden brown, facial hairs otherwise often dark ochraceous; inner surfaces tarsi light yellow; scopal hairs often golden-brown along margin. Terga 2–4 with apical pale fasciae extremely weak, thin, that of tergum 2 interrupted medially by more than one-third width of tergum. Pollen-collecting hairs as in *escondida* but trochanteral flocculus usually with more abundant hairs.

**MALE: Measurements and Ratios.**  $N = 20$ ; length, 7–9 mm; width, 1.5–2.5 mm; WL,  $M = 2.41 \pm 0.123$  mm; FL/FW,  $M = 0.96 \pm 0.006$ ; FS1/FS2,  $M = 1.85 \pm 0.045$ .

**Integumental Color.** As in female except as follows: wing membranes less infumate, veins often dark red; terga with apical areas translucent, ferruginous; sterna 2–5 narrowly hyaline apically.

**Structure.** Antennae short, female-like; flagellar segment 1 usually slightly shorter than in *escondida*, twice as long as segment 2, segment 3 distinctly longer than 2, broader than long, segments 4–7 usually slightly longer than broad; scape length as in female. Mandibles apposite, short, with subapical tooth. Maxillary palpus and segmental ratio as in female. Labial palpus as in female but ratio about as 1.0:0.5:0.5:0.5. Labral process about twice as long as broad, at least as long as labrum apical to process, bidentate, recurved, shiny. Clypeus sculptured as in female but punctures more abundant, separated mostly by one to three diameters. Face above antennal fossae with minute rugulae often strongly diverging towards ocelli. Vertex as in female. Genal area at least one and one-half times as broad as eye in profile, sculptured as in *escondida*. Pronotum with distinct humeral angles and weak lateral ridges. Thoracic sculpturing as in female. Metasomal terga sculptured as in female; sterna 2–5 tessellate, dull, with punctures mostly obscure. Terminalia (Figs. 22 and 23). Sternum 7 much as *escondida* but apical lobes slightly more separated; sternum 8 usually longer and narrower than in *escondida*.

**Vestiture.** White to pale ochraceous but inner surfaces of tarsi pale yellow and occasionally brown along inner margins of eyes and on vertex near ocelli. Metasomal terga 2–5 with apical pale fasciae extremely weak, that of tergum 2 interrupted medially by half width of tergum or more. Sterna 2–5 without dense subapical fimbriae of pale hairs.

**Type Material.** The holotype female of *pulverea* (PANS No. 4,043) was collected in California. The holotype female of *limnanthis* (USNM No 59,277) was collected at San Geronimo, Marin Co., California, April 23, 1913 by J.C. Bridwell.

**Distribution.** *Andrena pulverea* is known (Fig. 1) only from central California from Colusa County in the north to Merced County in the south. It has been collected from March 1 to June 2, but chiefly in late March and April. In addition to the types a total of 349 females and 93 males were examined from localities listed below (including records from the literature).

CALIFORNIA. CALAVERAS CO.: Angels Camp. COLUSA CO.: Bear Valley (9.7 mi. N of Highway 20). ELDORADO CO.: Alta. LAKE CO.: Middletown. MARIN CO.: Cypress Ridge; Fairfax; Olema (2 mi. S); Point Reyes; San Geronimo. MERCED CO.: Snelling (8 and 9 mi. NE). NAPA CO.: Pope Valley (and vicinity). SACRAMENTO CO.: Fair Oaks. SANTA CLARA CO.: Mt. Hamilton (5 mi. E); San Antonio Valley. SAN JOAQUIN CO.: Clements. SOLANO CO.: Dozier (11–12 mi. S of Dixon); Dixon (11 mi. S); Green Valley Estates. SONOMA CO.: Agua Caliente; Santa Rosa. STANISLAUS CO.: Evergreen Road (3.2 mi. W of Highway 120); La Grange (9 and 13 mi. NW). TUOLUMNE CO.: Chinese Camp; Mather (4–5 mi. S). YOLO CO.: Davis (and 5 mi. W).

**Floral Records.** *Andrena pulverea* is an oligoledge of flowers of the genus *Limnanthes* and has been collected from flowers of the plants listed below.

*Baeria* sp., *Blennospermum nannum*, *Limnanthes alba alba*, *L. douglasii*, *L. douglasii* var. *nivea*, *L. rosea*, *Montia perfoliata*, *Platystemon californicus*, *Ranunculus* sp., *Raphanus sativus*.

### *Andrena (Hesperandrena) duboisi* Timberlake

*Andrena (Hesperandrena) duboisi* Timberlake, 1951, Proc. United States Nat. Mus., 101:390–392.

*Andrena duboisi* is a small species marked by the lack of pronotal humeral angles and ridges, a metallic green integument (especially head and thorax), and galeae which are shiny and only extremely faintly shagreened. The male of *duboisi* can further be told from

either *A. escondida* or *A. pulverea* by the yellow marking on the clypeus as described below and by sterna 2–5 having subapical fimbriae of extremely short, white plumose hairs.

**FEMALE: Measurements and Ratios.** N = 20; length, 6.5–7.5 mm; WL, M =  $2.36 \pm 0.143$  mm; FL/FW, M =  $0.79 \pm 0.007$ ; FOVL/FOVW, M =  $2.85 \pm 0.050$ .

**Integumental Color.** Head and thorax metallic green except clypeus, scutellum, and metanotum often with violaceous reflections. Metasomal terga black with faint metallic green reflections; tergal apical areas hyaline apically to red or reddish brown basally; sterna without metallic reflections, apical areas more broadly hyaline. Wing membranes hyaline, yellow, veins red to reddish brown. Mandible with apical fifth to fourth rufescent; antennal flagellum brown below; tibial spurs light yellow.

**Structure.** Antennal scape as long as first four and one-third flagellar segments; flagellar segment 1 slightly longer than following two segments together; segment 2 about as long as 3 and shorter than 4; segments 5–7 about as long as broad. Eyes each three and two-thirds times as long as broad, inner margins parallel. Mandibles short, apposite, with subapical tooth. Malar space linear. Galea shaped as in *escondida*, surface shiny, faintly if at all shagreened. Maxillary palpus as in *escondida* but segmental ratio about as 0.8:1.0:0.8:0.7:0.5:0.7. Labial palpus as in *escondida* but ratio about as 1.0:0.5:0.5:0.7. Labral process short, two to three times as broad as long, weakly emarginate apically with rounded lateral angles; labrum apical to process about as long as process, moderately dulled by shagreening. Clypeus shaped as in *escondida*; dulled by fine tessellation and minute punctures separated mostly by about two puncture diameters except more crowded along apical margin. Supraclypeal area dulled by coarse tessellation. Face above antennal fossae with small parallel rugulae to ocelli. Facial fovea as in *escondida*. Vertex above lateral ocellus equals about half an ocellar diameter. Genal area in profile one and one-half times width of eye or slightly less, surface dull, shagreened.

Pronotum without humeral angle or lateral ridge or with only a trace of these structures; surface dull, shagreened. Mesoscutum as in *escondida* but punctures separated by one to three puncture widths except slightly more crowded peripherally. Scutellum and metanotum similar. Propodeum as in *escondida* but finely punctatorugose, basal area extremely narrow. Pleurae as in *escondida*.

Metasoma sculptured as in *escondida*, virtually impunctate. Pygidial plate as in *escondida* but usually more pointed, V-shaped with apex rounded. Sterna as in *escondida*.

**Vestiture.** White to pale ochraceous except as follows: facial fovea with tomentum pale brown in upper three-fourths or more, pale at lower end only; hind tarsi with inner surface pale yellow; terga 2–4 with distinct apical pale hair bands, that on tergum 2 interrupted medially by less than one-third width of tergum, terga 3 and 4 with bands complete. Pollen-collecting hairs as in *escondida*.

**MALE: Measurements and Ratios.** N = 9; length, 6.0–7.0 mm; width, 1.0–1.5 mm; WL, M =  $1.68 \pm 0.169$  mm; FL/FW, M =  $0.95 \pm 0.006$ ; FS1/FS2, M =  $2.10 \pm 0.087$ .

**Integumental Color.** As in female except as follows: clypeus with mediobasal pale yellow macula covering half of clypeus or more; head and thorax with metallic reflections blue or bluish green, mesoscutum occasionally with slight violaceous reflections; metasomal terga with metallic bluish green reflections on basal half of each tergum, hyaline apical margins broader than in female; distitarsi usually red.

**Structure.** Antennae short, female-like; flagellar segment 1 as long as 2 plus 3, which are subequal and shorter than 4, segments 5–8 as long as broad or slightly longer; scape as in female. Eyes each slightly longer than three times as long as broad, diverging



strongly towards vertex. Mandibles apposite, short, with subapical tooth. Galea as in female, shiny. Maxillary palpus as in female but segmental ratio about as 0.8:1.0:0.8:0.9:0.7:0.8. Labial palpus as in female but ratio about as 1.0:0.4:0.7:0.7. Labral process moderately long, about twice as broad as long, apical margin weakly emarginate, lateral teeth blunt, surface shiny; labrum apical to process about as long as process, dulled by shagreening. Clypeus sculptured as in female but minute punctures more abundant. Supraclypeal area as in female. Face above antennal fossae with parallel rugulae almost from inner eye margin to inner eye margin, in median third or less of facial area rugulae often diverge towards ocelli. Vertex short as in female. Pronotum with distinct humeral angles and complete lateral ridges, surface shagreened. Mesoscutum and scutellum sculptured much as in female. Propodeum as in female but surface outside of dorsal enclosure with punctures usually more distinct. Pleurae as in female.

Metasomal terga 1–6 sculptured as in female terga 1–5 but surfaces slightly shinier. Sterna much as in female. Sternum 7 has apical lobes broad and flattened, emargination much reduced. Sternum 8 with thick neck region, distinctly thicker than entire apical lobe.

**Type Material.** The female holotype (USNM No. 59, 279) of *Andrena duboisi* was collected at Davis, California, May 2, 1937 by J.J. DuBois.

**Distribution.** *Andrena duboisi* occurs in California (Fig. 1) from Colusa County in the north to San Diego County in the south. It has been collected from March 19 through May 12 and a total of 63 females and 9 males have been taken from localities listed below (including localities cited in the literature).

CALIFORNIA. ALAMEDA CO.: Niles. COLUSA CO.: Bear Valley (9.7 mi. N of Highway 20 and 13.5 km. N of Wilbur Springs). CONTRA COSTA CO.: Russelmann Park (Mt. Diablo); Walnut Creek. FRESNO CO.: Mendota. LOS ANGELES CO.: Los Angeles. MONTEREY CO.: Parkfield (6 mi. NE). SAN DIEGO CO.: San Diego. SAN FRANCISCO CO.: San Francisco. SAN LUIS OBISPO CO.: Simmler (15 mi. SE). SANTA BARBARA CO.: Christi Beach, Santa Cruz Island. SOLANO CO.: Dixon (9 mi. S); Dozier (11 mi. S of Dixon). STANISLAUS CO.: Turlock. TULARE CO.: Strathmore. YOLO CO.: Davis.

**Floral Records.** *Andrena duboisi* was collected at Davis by J.J. DuBois presumably at *Baeria* sp., according to Timberlake (1951). It has been collected from flowers listed below.

*Baeria* sp., *B. chrysostoma*, *Blennosperma nannum*, *Centromadia pungens*, *Lasthenia chrysostoma*, *Layia chrysanthemoides*, and *Limnanthes douglasii*.

### *Andrena (Hesperandrena) lativentris* Timberlake

*Andrena lativentris* Timberlake, 1951, Proc. United States Nat. Mus., 101:388.

*Andrena lativentris* is a small species with pronotal humeral angles and lateral ridges in both sexes (although weak in the females) and black integument. The female can be recognized by the broad facial fovea separated from the lateral ocellus by about half an ocellar diameter or a little more and by the mesoscutal and scutellar hairs being mostly shorter than the width of the flagellum, although longer peripherally and especially in anterior fifth of the mesoscutum. The male of *lativentris* is marked by a yellow clypeal macula and sterna 2–5 with distinct subapical fimbriae of long, curled, relatively sparse, pale hairs.

**FEMALE: Measurements and Ratios.** N = 20; length, 8.0–9.5 mm; width, 2.0–3.0 mm; WL,  $2.73 \pm 0.095$  mm; FL/FW,  $0.90 \pm 0.027$ ; FOVL/FOVW,  $2.78 \pm 0.56$ .

**Integumental Color.** Black except as follows: mandible with apical fourth rufescent; flagellum reddish brown below; wing membranes hyaline, not infumate, veins dark red or

reddish brown; metasomal terga 2–4 with apical areas broadly hyaline, colorless in apical fourth to third, reddened basally; tibial spurs pale yellow.

**Structure.** Antennal scape as long as first four flagellar segments or slightly more; flagellar segments as in *escondida*. Eyes each four times as long as broad, inner margins parallel. Mandibles short, apposite, with subapical tooth. Malar space short, linear. Galea as in *escondida*. Maxillary palpus as in *escondida* but segmental ratio about as 0.8:1.0:0.7:0.5:0.5:0.6. Labial palpus with ratio about as 1.0:0.5:0.4:0.4. Clypeus short, sculptured as in *escondida* but punctures extremely obscure. Supraclypeal area and face above antennal fossae sculptured as in *escondida*. Facial fovea extends below to just below a line at lower margins, antennal fossae two and one-fourth to two and one-third times as long as broad, separated from lateral ocellus by half an ocellar diameter or slightly more. Vertex above lateral ocellus short, equals about half an ocellar diameter or slightly more. Genal area in profile equals about one and one-third width of eye, surface dull, shagreened.

Pronotum without humeral angles and lateral ridges, surface dull, shagreened. Mesoscutum densely and finely tessellate, punctures minute, obscure, visible only at certain angles, separated by two or more puncture widths (slightly more crowded in anterior fifth and at extreme sides). Scutellum similar, not at all shiny. Propodeum declivous; dorsal enclosure tessellate, not at all punctatorugose; outside of enclosure with small sparse punctures; lateral carinae separated lateral from posterior surface complete. Pleurae dull, tessellate, punctures obscure, sculptured as in *escondida*.

Metasomal terga tessellate, dull, impunctate or punctures minute and obscure. Pygidial plate as in *escondida*. Sterna sculptured as in *escondida*.

**Vestiture.** White to pale ochraceous except as follows: facial fovea with tomentum silvery white to pale ochraceous, not brown in upper halves or more; metasomal terga 2–4 with white apical fasciae, that of tergum 2 narrowly interrupted medially; tergum 5 dark ochraceous medially. Pollen-collecting hairs as in *escondida*.

**MALE: Measurements and Ratios.** N = 15; length, 6.0–9.0 mm; width 2.0–3.0 mm; WL, M =  $2.44 \pm 0.224$  mm; FL/FW, M =  $0.94 \pm 0.014$ ; FSI/FS2, M =  $1.92 \pm 0.085$ .

**Integumental Color.** As in female except as follows: clypeus with large pale yellow maculae, dark laterally and apically; metasomal terga 2–5 with apical areas with at least apical halves hyaline, colorless; distitarsi rufescent.

**Structure.** Antennae short, female-like; flagellar segment 1 at least twice as long as segment 2, which equals segment 3, and broader than long; segments 4–7 about as long as broad; scape length as in female. Eyes three and one third times as long as broad, inner margins diverging towards vertex. Mandibles apposite, short, with subapical tooth. Galeae as in female. Maxillary palpus as in female but ratio about as 0.8:1.0:0.6:0.6:0.5:0.7. Labial palpus as in female but ratio about as 1.0:0.4:0.4:0.5. Labral process short, about twice as broad as long, emarginate, reflexed, shiny; labrum apical to process shorter than process. Clypeus dull, sculptured as in female. Supraclypeal area, face above antennal fossae and vertex as in female. Genal area as in female but only slightly broader than eye in profile.

Pronotum with weak humeral angles, lateral ridges present but weak, defined only above diagonal pronotal suture, dulled by fine shagreening. Thoracic sculpturing as in female but propodeum often finely punctatorugose at least basally; carina between lateral and posterior faces incomplete, short.

Metasomal terga sculptured as in female but surface slightly shiny, especially apical areas. Sternum 7 (Fig. 28) with lobes angulate laterally, apical imargination narrower. Sternum 8 (Fig. 29) with apical lobe entire, neck slightly broader than apical lobe, sternum thicker and broader than in *pulverea*.

**Vestiture.** White except inner surfaces of tarsi pale yellow. Metasomal tera 2–5 with relatively weak apical fasciae, broadly interrupted medially on tergum 2 and narrowly on tergum 3. Sterna 2–5 with distinct pale subapical fimbriae of long, sparse, curled, white hairs (as in *escondida* but longer and sparser).

**Type Material.** The holotype female of *lativentris* (USNM No. 59,278) was collected from flowers of *Baeria tenella* at Strathmore, Tulare Co., California, May 29, 1937.

**Distribution.** *Andrena lativentris* has been collected in California (Fig. 2) from Colusa County south to San Diego County. It has been taken from March 9 through July 5, but chiefly from late March into May. A total of 24 females and 17 males were examined from localities listed below (including localities cited in the literature).

CALIFORNIA. COLUSA CO.: Bear Springs (S of Leesville). CONTRA COSTA CO.: Mt. Diablo; Russelman Park. KERN CO.: no locality. NAPA CO.: Butts Canyon (0.5 mi. S. of Napa Co. line). RIVERSIDE CO.: Elsinore; Hemet Lake, San Jacinto Mts.; Herkey Creek, San Jacinto Mts. SAN DIEGO CO.: Cuyamaca Lake. SOLANO CO.: Dixon (9 mi. S); Dozier (11 mi. S. of Dixon). TULARE CO.: Earlimart; Goshen (5.6 mi. N); Strathmore. YOLO CO.: Davis.

**Floral Records.** *Andrena lativentris* is probably an oligolege of *Baeria* sp., but little is known concerning its floral preferences as yet. It has been collected from flowers of the following plants (records from the literature are included).

*Baeria* sp., *B. gracilis*, *B. tenella*, *Blennospermum nannum*, *Lasthenia chryostoma*, *Layia chrysanthemoides*, *L. platyglossa*.

### *Andrena (Hesperandrena) baeriae* Timberlake

*Andrena baeriae* Timberlake, 1941, Bull. Southern California Acad. Sci., 39:194.

*Andrena (Hesperandrena) baeriae*: Lanham, 1949, Univ. California Publ. Ent., 8:208.

*Andrena baeriae* differs from females of the preceding species by the distinct pronotal angles and lateral ridges. As in *lativentris* the integument is black (occasional slight metallic tints may be present on the frons) and the facial fovea is broad, being separated from the lateral ocellus by less than one ocellar diameter. The female is often marked with brown hairs posteromedially on the mesoscutum and medially on the scutellum, as well as on the face along the inner margins of the eyes. The male of *baeriae* has (Fig. 10) pronotal angles and ridges (the integument posterior to the lateral ridge is frequently less shagreened and moderately shiny) and has sterna 2–5 with weakly formed subapical fimbriae of long hairs as described below.

**FEMALE: Measurements and Ratios.** N = 5; length, 8.5–10.0 mm; width, 2.5–3.0 mm; WL, M =  $2.72 \pm 0.159$  mm; FL/FW, M =  $0.91 \pm 0.013$ ; FOVL/FOVW, M =  $1.90 \pm 0.045$  mm.

**Integumental Color.** Integument black except as follows: frons above antennal fossae occasionally with slight metallic tints; mandibles with apical hyaline, veins red to reddish brown; metasomal terga narrowly hyaline apically, becoming dark towards base of apical area; tibial spurs pale yellow.

**Structure.** Antennal scape length about equal to first four flagellar segments; flagellar segment 1 as long as segments 2 plus 3, which are equal in length; segments 5–7 quadrate. Eyes each about four times as long as broad, inner margins parallel. Mandibles apposed, short, with subapical tooth. Malar space and galeae as in *escondida*. Maxillary palpus as in *escondida* but segmental ratio about as 0.8:1.0:0.7:0.6:0.5:0.6. Labial palpus as in *escondida* but ratio about as 1.0:0.5:0.6:0.6. Labrum as in *escondida* but usually gently emarginate apically. Clypeus, supraclipeal area and face above antennal fossae as



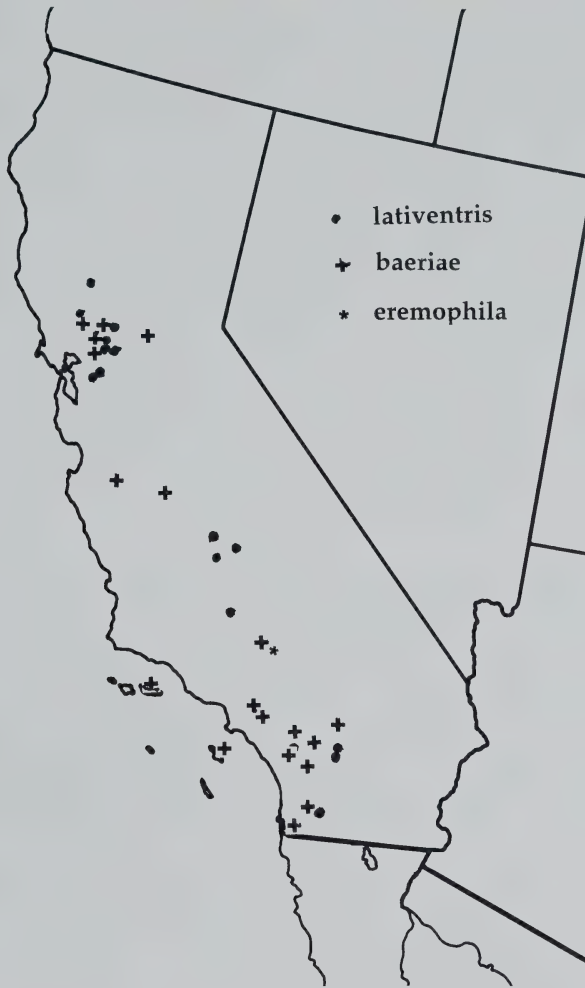


Fig. 2. Map showing the known distributions of *A. lativentris*, *A. baeriae*, and *A. eremophila*, n. sp.

in *escondida*. Facial fovea broad, separated from lateral ocellus by one ocellar diameter or somewhat more, extending below to well beyond a line across lower margins of antennal fossae. Genal area in profile almost one and one-half times as broad as eye, surface dull, shagreened.

Pronotum with humeral angles and lateral ridges (Fig. 10). Mesoscutum dull, tessellate, punctures sparse and obscure. Mesoscutum dull, tessellate, punctures sparse and obscure. Scutellum similar. Propodeum and pleurae as in *escondida*.

Metasomal terga sculptured as in *escondida*. Pygidial plate as in *escondida*, without raised rim in specimens at hand. Sterna 2–5 sculptured as in *escondida*.

**Vestiture.** White to pale ochraceous except as follows: along inner margins eyes and upper face dark ochraceous to brown; facial fovea with tomentum dark brown; mesoscutum and scutellum often with pale yellow hairs; apices of femora and tibial plates occasionally with brown hairs; terga 5 and 6 with brown hairs at least medially; tarsi with inner surfaces with pale yellow hairs. Mesoscutum and scutellum with hairs mostly longer than width of flagellum, relatively sparse; metasomal tergum 2 with apical pale fascia interrupted medially. Pollen collecting hairs as in *escondida*.

**MALE: Measurements and Ratios.** N = 11; length 6–8 mm; width, 1.5–2.0 mm; WL, M =  $2.27 \pm 0.370$  mm; FL/FW, M =  $0.95 \pm 0.026$ ; FSI/FS2,  $2.24 \pm 0.026$ .

**Integumental Color.** As in female except as follows: terga 2–5 with apical areas more broadly hyaline apically, often half of apical area colorless; tergum 2 laterally usually with small, subapical, yellow spot surrounded by rufescent border, terga 1 and 3 rarely with similar spots but usually rufescent or reddish brown and without yellow.

**Structure.** Antennae short, female-like; flagellar segment 1 twice as long as segment 2, which is about as long as segment 3 and broader than long; segments 4–7 about as long as broad; scape length as in female. Eyes each about three and one-half times as long as broad or slightly longer, inner margins diverging towards vertex. Mandibles slightly decussate, short, with subapical tooth. Galeae as in female. Maxillary palpus as in female but ratio about as 0.8:1.0:0.8:0.5:0.5:0.6. Labial palpus as in female but ratio about as 1.0:0.5:0.4:0.5. Labral process and labrum as in *escondida*. Clypeus sculptured as in female but punctures slightly denser, separated largely by one to two puncture widths or less. Supraclypeal area as in female. Face above antennal fossae with rugulae as in female but diverging upward immediately below ocelli. Vertex and genal area as in female.

Pronotum with distinct humeral angles and lateral ridges, surface dulled by shagreening anterior to lateral ridge and shiny to moderately shiny posterior to ridge. Thoracic sculpturing as in female.

Metasomal sculpturing as in female but terga 1–5 slightly shinier. Sterna as in female. Sterna 7 and 8 small, sternum 7 (Figs. 13, 28) with emargination relatively deep and narrow, sides angulate near the apical margin; sternum 8 (Fig. 29) much as in *lativentris* but much smaller and narrower.

**Vestiture.** White to pale ochraceous but inner surfaces of tarsi pale yellow. Metasomal terga 2–5 with weak apical pale fasciae, those on terga 2 and 3 interrupted medially often by one-third width of tergum or more. Sterna 2–5 with distinct subapical fimbriae of long, curled, sparse hairs, individually each separated by two or more hair-widths so that distinct dense white bands not formed (as in *lativentris*).

**Type Material.** The holotype female (CAS No. 14,349) of *baeriae* was collected from flowers of *Baeria chrysostoma* var. *gracilis* and *B. aristata* at Riverside, California, from March 29 to April 6 by P.H. Timberlake.

**Distribution.** *Andrena baeriae* is known (Fig. 2) from San Diego County north to Yolo County, California. It has been collected from March 3 to July 5, but chiefly in late March into May. A total of 94 females and 16 males from the localities listed below (including records from the literature) were examined. La Mesa, San Diego County listed below is the probable locality for a single male labelled as from La Mesa, in Baja California, Mexico. However, the authors cannot find such a locality in Baja California. La Mesa in San Diego County, California, on the other hand, lies about 3 miles east of the San Miguel Mission in San Diego County which is mentioned on the original label and also not far from San Miguel Mountain. We conclude that an error was made on the hand-written label by the collector (T.D.A. Cockerell).

CALIFORNIA. KERN CO.: Rosamond (hills N of). FRESNO CO.: Mendota. LOS ANGELES CO.: Puente Hills; Santa Catalina Island; Whittier. NAPA CO.: Aetna springs (N. of Butts Canyon). RIVERSIDE CO.: Gavilan; Lake Perris; Riverside; Sta. Rosa Plateau Reserve (WSW of Murrieta). SACRAMENTO CO.: Folsom. SAN BENITO CO.: Hollister (35 mi. S). SAN BERNARDINO CO.: Morongo Valley. SAN DIEGO CO.: Lake Cuyamaca; La Mesa (3 mi. E of San Miguel Mission). SANTA BARBARA CO.: Christi Beach, Sta. Cruz Island. SOLANO CO.: Dixon (9 and 11 mi. S). YOLO CO.: Davis.

**Floral Records.** *Andrena baeriae* is probably an oligolege of flowers of the genus *Baeria* but little is actually known of its pollen preferences. It has been collected from

flowers of the plants listed below (including records from the literature).

*Baeria* sp., *B. aristata*, *B. chrysostoma* var. *gracilis*, *Layia* sp., *L. chrysanthemoides*.

***Andrena (Hesperandrena) leucomystax*, new species**

*Andrena leucomystax* is a small species with distinct pronotal angles and lateral ridges in both sexes. It differs from *lativentris* in both sexes by having distinctly metallic green integument on the face and mesoscutum, by having the scutellum and often the postero-medial area of the mesoscutum shiny with shagreening slight or absent. The female has metasomal terga 2 and 3 with apical pale fasciae that are much as in *escondida* or *baeriae*. The male has a dense beard of long white hairs on the mostly pale yellow clypeus and sterna 2–5 short white subapical fimbriae narrowly interrupted medially (usually by less than one-third width of tergum).

**FEMALE: Measurements and Ratios.** N = 20; length, 7.0–8.5 mm; width, 2.0–3.0 mm; wing length, M =  $2.41 \pm 0.150$  mm; FL/FW, M =  $0.86 \pm 0.006$ ; FOVL/ FOVW, M =  $2.99 \pm 0.077$ .

**Integumental Color.** Black except as follows: frons above antennal fossae with greenish metallic tints; mandible with apical third to half rufescent; flagellar segments 3–10 dark red below, segments 1 and 2 dark brown; mesoscutum with anterior third with metallic green tints; wing membranes hyaline, yellowed, veins red to reddish brown; metasomal terga hyaline apically, becoming dark towards base of apical area, usually without metallic tints basally; tibial spurs testaceous.

**Structure.** Antennal scape as in *baeriae*. Eyes as in *baeriae* but diverging slightly towards vertex. Mandibles and malar space as in *escondida*. Face sculptured much as in *escondida* and *baeriae*. Galeae as in *escondida* except surface shiny, not at all tessellate or shagreened. Maxillary palpus short as in *baeriae*, segmental ratio about as 1.0:0.8:0.6:0.5:0.3:0.4. Labrum as in *baeriae*, with process short, broad, gently emarginate apicomediaally. Clypeus, supraclypeal area and face above antennal fossae as in *escondida* but face above antennal fossae with longitudinal rugulae relatively coarse. Facial fovea relatively short and narrow, separated from lateral ocellus by one ocellar diameter or slightly more. Vertex above lateral ocellus equal to half an ocellar diameter. Genal area as in *baeriae*.

Pronotum with humeral angles and lateral ridges well formed, space posterior to lateral ridge relatively shiny. Mesoscutum usually shiny and without shagreening posteromedially, otherwise as in *baeriae*. Scutellum usually without shagreening, shiny, with punctures scattered peripherally (Fig. 19). Propodeum and pleurae as in *escondida*.

Metasomal terga sculptured much as in *escondida* or *baeriae* but tergum 1 not densely tessellate, rather coarsely shagreened, and terga 2–4 with basal areas usually moderately shiny, shagreened but not densely so. Sterna 2–5 sculptured much as in *escondida*.

**Vestiture.** White to pale ochraceous except as follows: facial fovea with tomentum pale brown to dark ochraceous; vertex and thoracic dorsum with hairs ochraceous to yellow; terga 2–4 with white apical fasciae, those on terga 2 and 3 narrowly interrupted medially usually by distinctly less than one-third width of tergum; terga 5 and 6 with vestiture white. Pollen collecting hairs as in *escondida* (Figs. 16 to 18).

**MALE: Measurements and Ratios.** N = 20; length, 6.0–8.0 mm; width 1.2–2.0 mm; wing length, M =  $2.26 \pm 0.190$  mm; FL/FW, M =  $0.93 \pm 0.007$ ; FS1/FS2, M =  $2.09 \pm 0.034$ .

**Integumental Color.** As in female except as follows: clypeus pale yellow except narrow infuscation along posterior border and in lateral angles and dark apical border;



terga 1–3 basal areas without lateral pale spots; face above antennal fossae and anterior third of mesoscutum with metallic green reflections.

**Structure.** Antennae short, female-like; flagellar segment 1 as long as segments 2 and 3 together or slightly longer; segment 2 subequal in length to segment 3; segments 4–6 about as long as broad, remaining segments distinctly longer. Eyes, mandible, and genal area as in *baeriae*. Galea as in female, surface shiny, unshagreened. Maxillary palpus as in female, ratio about as 1.0:1.0:0.8:0.6:0.4:0.8. Labial palpus as in female but segmental ratio about as 1.0:0.6:0.7:0.6. Labral process somewhat recurved, distinctly toothed. Clypeus sculptured as in female, but punctures not evident due to pale color. Supraclypeal area and face above antennal fossae sculptured as in female. Vertex and genal area as in female.

Pronotum with distinct humeral angles and lateral ridges, surface anterior to ridge tessellate, dull, posterior to ridge moderately shiny. Mesoscutum usually with small posteromedian area shiny, unshagreened; scutellum usually shiny, unshagreened or relatively faintly so.

Metasomal sculpturing as in female but terga 2–5 usually slightly shinier. Sterna as in female. Sternum 7 (Fig. 30) similar to that of *duboisii* (Fig. 24) but apical lobes broader and slightly slanted from the apex, median emargination slightly deeper; sternum 8 (Fig. 31) with apical lobe entire, neck region much broadened posteriorly as in *duboisii* (Fig. 25).

**Vestiture.** White to pale ochraceous but inner surfaces of tarsi pale yellow. Metasomal terga 2–5 with white apical fasciae usually interrupted medially on terga 2–4 as in *baeriae*. Sterna 2–5 with weak subapical fimbriae of extremely short, white, plumose hairs (as in *duboisii*).

**Type Material.** The holotype female and allotype male with one female paratype of *leucomystax* were reared from a nest site located at 9 miles S of Dixon, Solano County, California, October 18, 1968 by B.J. Donovan. The holotype and allotype are deposited in the collection of the California Academy of Sciences.

**Distribution.** *Andrena leucomystax* is known (Fig. 3) only from California. In addition to the type series associated with the holotype, 27 female and 24 male paratypes (CAS, UCD, UCR, LACM, USU, INHS) from California were collected as follows:

CALIFORNIA. FRESNO CO.: Coalinga (14.5 mi. N).— 1 female, Mar. 21, 1963, J.W. MacSwain. Mendota.— 4 females, March 22, 1967, R.R. Snelling; 2 males, March 14, 1957 from *Baeria* sp., R.R. Snelling. SAN LUIS OBISPO CO.: Simmler (15 mi. SE at south end of Soda Lake).— 1 male, March 2, 1969, H.B. Leach. SOLANO CO.: Dixon (9 mi. S).— 2 males on *Layia chrysanthemoides*, April 17, 1969, R.W. Thorp; 2 males, April 11, 1975, R.B. Kimsey; 1 male, April 24, 1969, R.W. Thorp; 2 females, April 27, 1949, W.F. Chamberlain on *L. chrysanthemoides*. Dozier (11 mi. S of Dixon).— 1 female on *Blennospermum nanum* Mar. 26, 1969, R.W. Thorp; 1 female, 1 male on *Limnanthes douglasii*, Mar 26, 1969, B.J. Donovan; 1 female on *Lasthenia chrysostoma*, April 3, 1969, B.J. Donovan; 1 female on *B. nanum*, Apr. 3, 1969, D.L. Briggs; 1 female, 2 males on *B. nanum*, March 19, 1969, R.W. Thorp; 3 females on *L. chrysostoma*, Apr. 17, 1969, R.W. Thorp; 5 females on *L. chrysostoma*, May 1, 1969, D.L. Briggs; 1 male on *B. nannum*, March 8, 1969, B.J. Donovan; 1 male, April 3, 1971, R.W. Thorp; 2 males on *B. nannum*, March 26, 1969, B.J. Donovan; 1 male on *B. nannum*, April 11, 1969, B.J. Donovan; 2 males on *L. chrysostoma*, April 3, 1969, B. J. Donovan; 2 males, April 3, 1969, J. Marsh; 1 male at nest, May 1, 1969, R.W. Thorp; 1 female on *B. nannum*, March 19, 1969, B.J. Donovan; 2 males on *Downingia pulchella*, April 24, 1969, R.W. Thorp; 1 female on *L. lasthenia*, May 1, 1969, R.W. Thorp; 1 male at nest site, April 3, 1969, B.J. Donovan; 1 female at nest site, May 1, 1969, B.J. Donovan. STANISLAUS CO.: LaGrange.— 1 female on *Baeria* sp., April 26, 1952, R. Snelling. TULARE CO.: Strathmore.— 1 female on

*Baeria tenella*, March 28, 1937, P.H. Timberlake. YOLO CO.: Davis.— 1 female, May 12, 1937, J.J. DuBois. Winters.— 1 female on *Baeria* sp., March 6, 1947, G.E. Bohart.

*Andrena (Hesperandrena) dissona*, new species

*Andrena dissona* is a small bee which has a distinct pronotal humeral angle and lateral ridge in both sexes. The female can be distinguished from that of other species with distinct pronotal angle and ridge by having a black, moderately shiny to shiny mesoscutum and scutellum, the apical fascia of tergum 2 usually broadly interrupted medially and has the mesoscutal punctures (especially just inside of parapsidal lines) more distinct and more crowded. The male has a partly yellow clypeus and sterna 2–5 with subapical fimbriae of long, down-curved, weakly plumose, relatively sparse hairs.

**FEMALE: Measurements and Ratios.** N = 5; length, 7.0–7.5 mm; width, 2.25–2.50 mm; wing length,  $2.44 \pm 0.287$  mm; FL/FW, M =  $0.85 \pm 0.011$ ; FOVL/FOVW, M =  $2.63 \pm 0.16$ .

**Integumental Color.** Black except as follows: metallic tints occasionally present on face above antennal fossae but absent on mesonotum and mesepisternum; metasomal terga with apical areas entirely or largely hyaline, clear to yellowish; terga 1 and 2 with basal areas with small, apical, brownish yellow, apicolateral spots, with a narrow yellowish line connecting spots across tergum; sterna with apical areas hyaline; wing membranes hyaline, veins reddish brown.

**Structure.** Antennal scape equal to or slightly less than first four flagellar segments; flagellar segments as in *baeriae* but segments 5–9 about as long as broad or slightly longer, segment 10 distinctly longer than broad. Mandibles, malar space and galeae as in *baeriae* but galeae shinier, shagreening delicate (not as shiny as in *perdissona*). Labrum short and broad as in *baeriae* but usually not emarginate apicomediaally. Maxillary palpus as in *escondida* but segmental ratio about as 1.0:1.0:0.8:0.6:0.4:0.7. Labial palpus as in *escondida* but ratio about as 1.0:0.6:0.4:0.7. Clypeus, supraclypeal area and face above antennal fossae as in *escondida* but clypeal punctures somewhat more abundant in apical half and more distinct. Facial fovea and genal area as in *baeriae*. Vertex above lateral ocellus equals about half an ocellar diameter.

Pronotum with distinct humeral angles and lateral ridges. Mesoscutum moderately shiny, shagreening coarse; punctures moderately well formed, in area just mesad of parapsidal line mostly separated by one puncture width or slightly less. Scutellum similar but occasionally shagreening less distinct, moderately shiny. Propodeum and pleurae as in *escondida*.

Metasomal terga sculptured as in *escondida*. Pygidial plate as in *escondida*, with broad raised rim especially in apical two-thirds. Sterna 2–5 as in *escondida*.

**MALE: Measurements and Ratios.** N = 15; length, 6.5–7.0 mm; width, 2.0–2.5 mm; wing length, M =  $2.23 \pm 0.128$  mm; FL/FW, M =  $0.86 \pm 0.007$ ; FS1/FS2, M =  $2.13 \pm 0.065$ .

**Integumental Color.** Black except as follows: clypeus with cream-colored or pale yellow mediobasal macula, apical third or fourth and lateral angles of clypeus black; face above antennal fossae and mesepisterna often with faint metallic reflections; flagellum below dark reddish brown; wing membranes hyaline, clear, veins reddish brown; metasomal terga and sterna with apical areas hyaline, colorless to slightly yellowed basally.

**Structure.** Antennae short, female-like; flagellar segment 1 longer than segments 2 plus 3, segment 2 subequal in length to 3 which is slightly shorter than 4, segments 5–10 about as long as broad, 11 distinctly longer than broad. Eyes each about one and one-half



Fig. 3. Map showing the known distributions of *A. leucomystax*, n. sp.; *A. dissona*, n. sp.; and *A. compositarum*, n. sp.

times as long as broad, inner margins diverge towards vertex. Mandibles and galeae as in *baeriae*. Maxillary palpus as in female but segmental ratio about as 1.0:1.0:0.7:0.6:0.4:0.7. Labial palpus as in *baeriae* but ratio about as 1.0:0.3:0.2:0.3. Labral process and labrum as in *escondida* but not at all or only slightly emarginate apicomediaally. Clypeus as in *baeriae* but punctures hardly visible. Supraclypeal area and face above antennae as in *baeriae*. Vertex above lateral ocellus equals about half an ocellar diameter.

Pronotum with distinct humeral angles and lateral ridges much as in *baeriae*. Thoracic sculpturing as in female but scutellum occasionally moderately shiny, shagreened.

Metasomal sculpturing as in female but terga 3–5 moderately shiny. Sterna as in female. Sternum 7 (Fig. 32) with apical lobes narrow, sides not strongly angulate, emargination deep and narrow; sternum 8 (Fig. 33) much as in *lativentris* but much smaller.

**Vestiture.** White to pale ochraceous but on inner surfaces of tarsi yellow and on dorsum of thorax often slightly darker ochraceous. Metasomal terga 2–5 with weak apical pale fasciae, those on terga 2 and 3 interrupted medially, usually by more than a third of width of tergum. Sterna 2–5 with subapical fimbriae of relatively sparse, long, curved downward, plumose hairs.



**Type Material.** The holotype female of *dissona* (CAS) was collected at Strathmore, Tulare Co., California, from flowers of *Baeria chrysostoma*, March 29, 1937 by P.H. Timberlake. The allotype male of *dissona* (CAS) was collected at Earlimart, Tulare County from flowers of *Baeria terrella*, March 9, 1937 by P.H. Timberlake. Four female and fifteen male paratypes from California (Fig. 3) (UCB, UCD, INHS, CAS, LACM) are as follows:

CALIFORNIA. SOLANO CO.: Dixon (9 mi. S).— 1 male, April 24, 1969 from *Layia chrysanthemoides* or *Baeria chrysostoma*, B.J. Donovan; 1 male, April 24, 1969 from *L. chrsanthemoides* or *B. chrysostoma*, R.W. Thorp; 1 male April 17, 1969 from *L. chrysanthemoides*, R.W. Thorp; 1 male April 17, 1969, from *L. chrysanthemoides* D.L. Briggs. Dixon (11 miles S at Dozier).— 1 male April 17, 1969, from *Layia chrysanthemoides*, D.L. Briggs. YOLO CO.: Davis.— 1 male, May 12, 1937, M. DuBois.

### *Andrena (Hesperandrena) eremophila*, new species

This modest-sized species is known only from specimens of the female sex all collected at one locality. Like the females of *A. escondida*, these females do not have pronotal angles nor pronotal dorsolateral ridges, nor do they have metallic reflections in the dark color. They differ from females of *escondida* by having a larger, coarsely rugulose apical clypeal area and by having the metasomal terga (especially the first three) shinier due to the more fragile and less dense shagreening.

**FEMALE: Measurements and Ratios.** N = 5; length, 8–9 mm; width, about 3 mm; wing length,  $2.41 \pm 0.093$  mm; FL/FW, M =  $0.93 \pm 0.007$ ; FOVL/FOVW, M =  $3.20 \pm 0.273$ .

**Integumental Color.** Black except as follows: mandible with apical third to half rufescent; flagella slightly reddened below; wing membrane hyaline, veins brown to reddish brown; metasomal terga with apical areas half or more hyaline, basal areas often with rufescent areas present apically; tibial spurs yellow.

**Structure.** Scape as long as first four flagellar segments or slightly more; flagellar segment 1 longer than segments 2 plus 3 which are about equal in length and broader than long; segments 4–8 as broad as long or slightly longer. Eyes, mandibles, and malar space as in *escondida*. Galea pointed, outer margin apical half gently concave; surface moderately shiny, tessellation extremely fine. Maxillary palpus exceeds galea by last two segments, segmental ratio about as 1.0:1.4:0.5:0.4:0.4:0.5. Labial palpus normal, segmental ratio about as 0.8:1.2:0.3:0.4. Labral process about three times as broad as long, shallowly emarginate medially, labrum apical to process slightly shorter, shallowly, transversely grooved, moderately shiny. Clypeus gently rounded from side to side, surface in basal half or slightly more dull, tessellate with relatively sparse, small punctures; apical third to half moderately shiny, coarsely reticulorugose. Supraclypeal area, face, and facial foveae much as in *escondida*.

Pronotum without humeral angle or dorsolateral ridges, surface dull, shagreened. Mesoscutum and scutellum as in *escondida*. Propodeum and pleurae as in *escondida*. Metasomal terga sculptured as in *escondida*. Pygidial plate and sterna as in *escondida*.

**Vestiture.** Essentially as described for the female of *escondida*.

**Type Material.** The female holotype of *eremophila* (USU) and the three female paratypes were collected at Mojave, Kern County, California, April 10, 1936 by G.E. and R.M. Bohart (Fig. 2). One female paratype was collected at the same locality April 11, 1938 by G.E. and R.M. Bohart. Paratypes will be deposited at the following institutions: USU, OSU (Oregon State Univeristy), CAS, INHS.

*Andrena (Hesperandrena) compositarum*, new species

*Andrena compositarum* is a relatively small species similar to *A. escondida*. However, the female of *compositarum* has the pronotum with complete pronotal angles and dorsoventral ridges, although these may be weak. The female of *compositarum* can be distinguished by the facial foveae being covered with brown to dark brown hairs and the dorsum of the thorax having at least some brown hairs. The male of *compositarum* can be separated from that of *escondida* by having a black clypeus, weak but distinct pronotal angles and dorsolateral ridges, and sterna 2–5 with subapical fimbriae consisting of very long, curved hairs, longer than in *escondida* males but not as dense nor as white.

**FEMALE: Measurements and Ratios.** N = 6; length, 9–9.5 mm; width, 2.0–2.5 mm; WL, M =  $2.69 \pm 0.080$  mm; FL/FW, M =  $0.891 \pm 0.008$ ; FOVL/FOVW, M =  $2.34 \pm 0.061$ .

**Integumental Color.** As in *escondida* in all particulars.

**Structure.** Antennal scape as long as first four flagellar segments or almost so; flagellar segment 1 as long as following three segments or slightly shorter, segments 2 and 3 shorter than broad, of equal length, and slightly shorter than segment 4; segments 5 to 7 or 8 about as long as broad. Eyes, mandibles as in *escondida*; malar space surpassing tip of galea to slightly shorter; segmental ratio about as 0.5:0.7:0.5:0.5:0.4:0.5. Labial palpus normal, segmental ratio about as 0.9:0.4:0.4:0.5. Labral process short, distinctly but shallowly emarginate; labrum apical to process flat to rounded, dull, often base (near process) with weak, short, longitudinal rugulae, finely tessellate. Clypeus, supraclypeal area and face sculptured as in *escondida*. Facial fovea extends to distinctly below lower margins of antennal fossae. Genal area (head in profile) more than twice as broad as eye, sculptured as in *escondida*.

Pronotum with humeral angles and dorsolateral ridges, but relatively weak. Mesoscutum and scutellum with small distinct punctures separated by one to two or three puncture widths, dulled by distinct tessellation. Scutellum as in *escondida* but basal area not reticulorugose, slightly roughened more than the general tessellation. Mesopleurae dull, tessellate, with scattered small but distinct punctures separated by two to four or more puncture widths.

Metasomal terga sculptured as in *escondida*; pygidial plate as in *escondida* but not as distinctly U-shaped, more V-shaped with rounded apex. Sterna sculptured as in *escondida*.

**Vestiture.** Pale ochraceous to ochraceous except as follows: facial foveae with short brown tomentum, paler on lower third or less; mesoscutum and scutellum with some brown hairs medially, usually largely brown; scopal hairs along posterior margin of tibia and basitarsis usually pale brown to brown. In other respects vestiture as *escondida*.

**MALE: Measurements and Ratios.** N = 11; length, 8–9 mm; WL, M =  $2.60 \pm 0.086$  mm; FL/FW, M =  $0.94 \pm 0.010$ ; FS1/FS2, M =  $2.35 \pm 0.081$ .

**Structure.** Antennae as in *escondida* but flagellar segment 2 equal to or slightly shorter (allotype) than segment 3. Eyes each about three and a half times as long as broad, inner margins diverging strongly towards vertex. Mandibles and galeae as in *escondida*. Maxillary palpus short, exceeding galea by no more than last maxillary palpal segment, segmental ratio about as 7.0:7.0:4.5:4.0:3.5:3.5. Labial palpus with segmental ratio as 9.0:4.0:3.0:4.0. Labral process deeply emarginate apically, lateral teeth curved down, sharp; labrum apical to process (measured from tips of apical teeth) distinctly shorter than process, shiny. Clypeus, supraclypeal area, face and vertex above ocelli as in female. Genal area broad, in profile, one and one-half times as wide as width of eye or slightly longer. Pronotum with distinct lateral angles but dorso-ventral ridge weak, especially in

lower half, sculpture of thorax as in female. Metasomal terga sculptured much as in female but shagreening weaker and surfaces shinier, especially on terga 3–6.

Sternal sculpturing as in female. Sternum 7 with apical lobes rounded, emargination narrow, moderately deep. Sternum 8 with apical lobe short, shallowly emarginate medially, neck region almost parallel-sided, slightly broader than apical lobe.

**Vestiture.** Generally white to pale ochraceous, not brown on face or thoracic dorsum as in female. Terga 2–5 with distinct subapical fimbriae consisting of long, relatively sparse hairs (especially laterally) which curve downward, unlike the dense white bands of straight shorter hairs of *escondida*.

**Type Material.** The holotype female (UCD), allotype male (UCD), one female and one male paratype (INHS) of *compositarum* were collected from *Layia chrysanthemoides* at Dixon (9 miles S), Solano Co., California, by R.W. Thorp on April 17, 1969. The holotype and allotype are deposited in the California Academy of Natural Sciences. Paratypes are in the collections of the University of California at Davis and the Illinois Natural History Survey in Champaign. Four female and nine male paratypes were collected from California (Fig. 3) as follows:

SOLANO CO.: Dixon (9 mi. S). 1 female, May 8, 1969 from *Layia chrysanthemoides*, R.W. Thorp; 1 female, May 1, 1969, from *L. chrysanthemoides*, B.J. Donovan; 1 female, 1 male, April 24, 1969 from *L. chrysanthemoides*, R.W. Thorp; 2 males from *L. chrysanthemoides*, April 24, 1969, B.J. Donovan. STANISLAUS CO.: LaGrange (1 mi. N). 1 female, 4 males, S.M. Fullerton; LaGrange (3 mi. N). 2 males, Mar. 26, 1960, S.M. Fullerton.

## INDEX OF SPECIES NAMES

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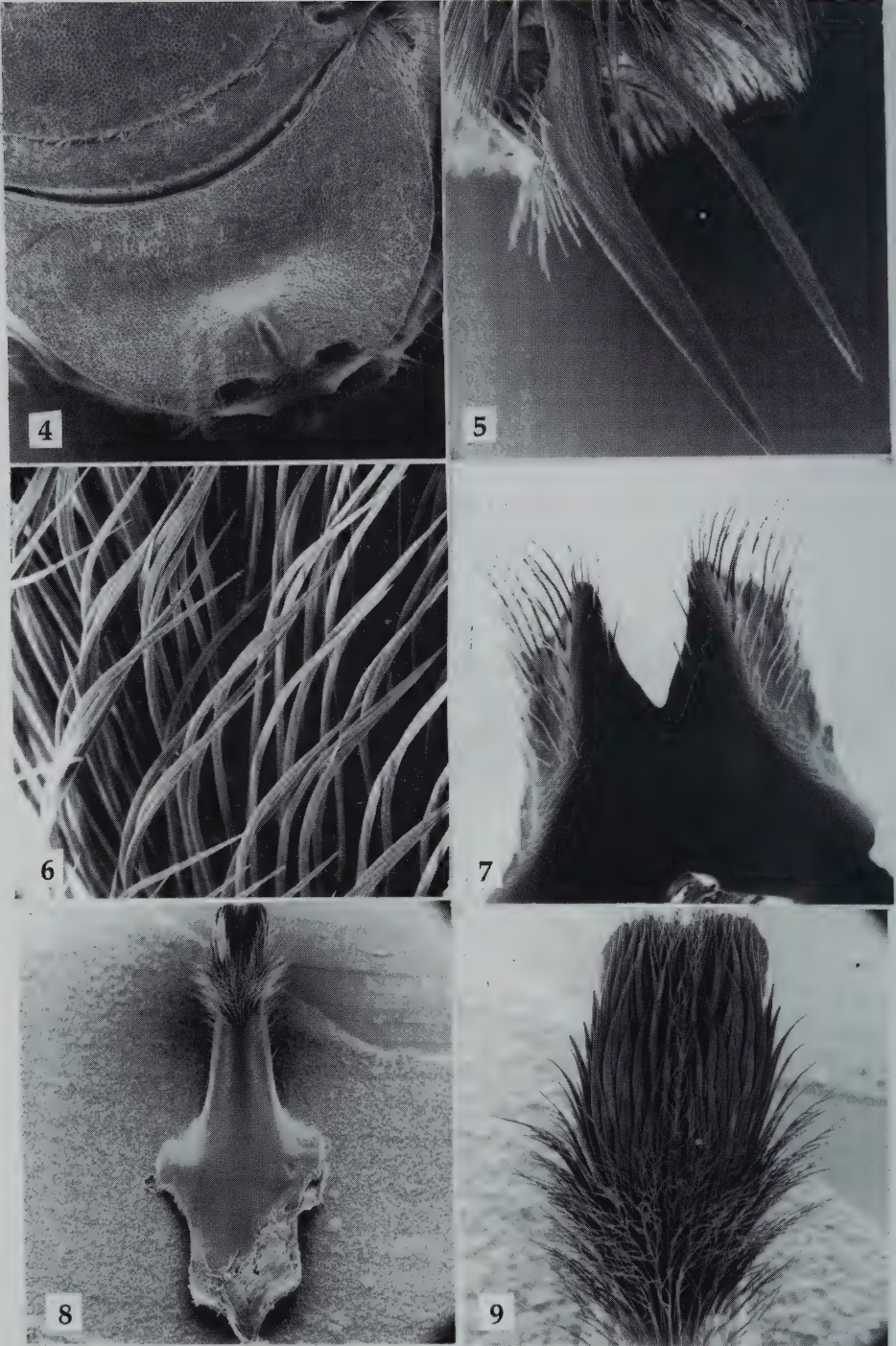


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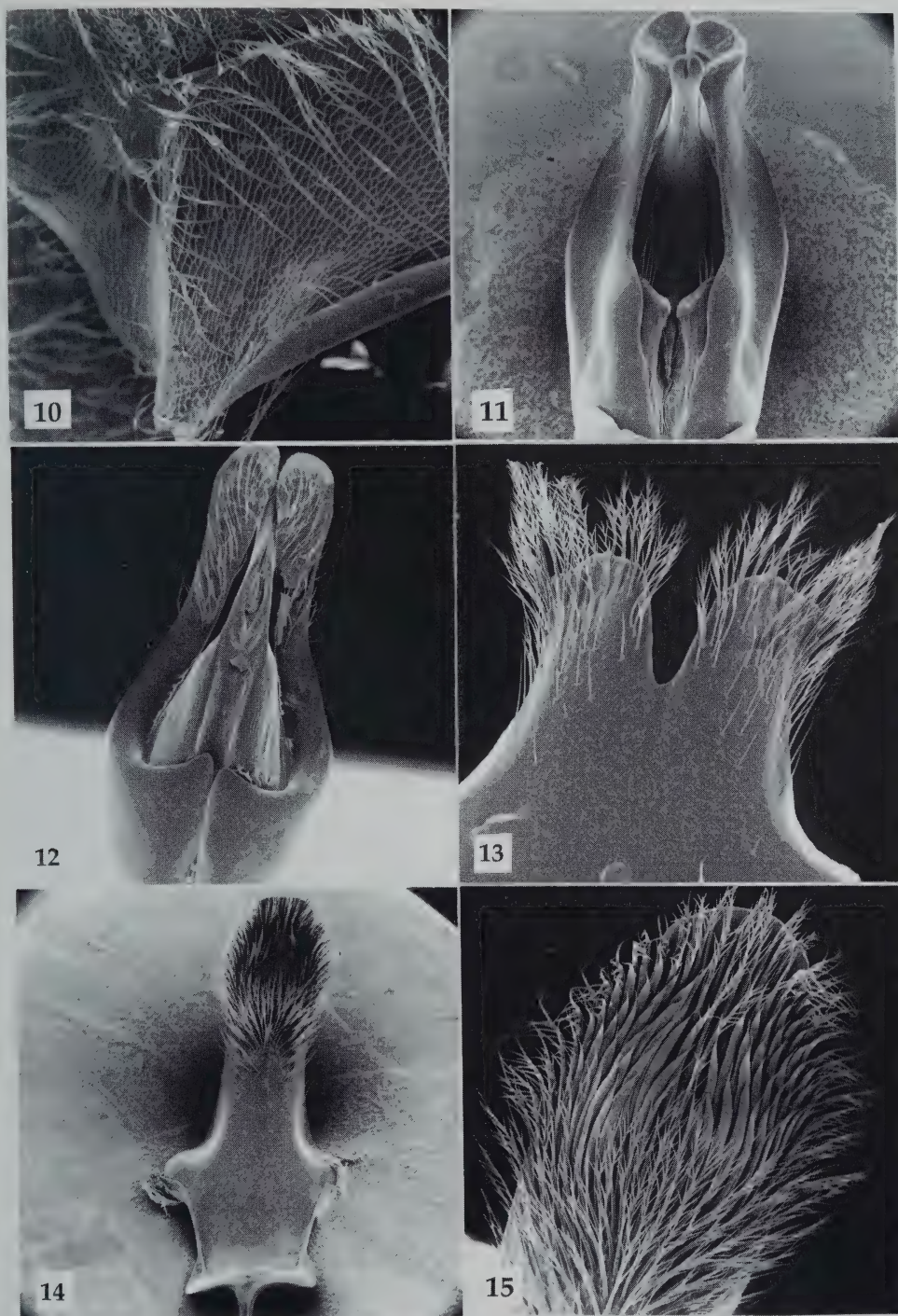
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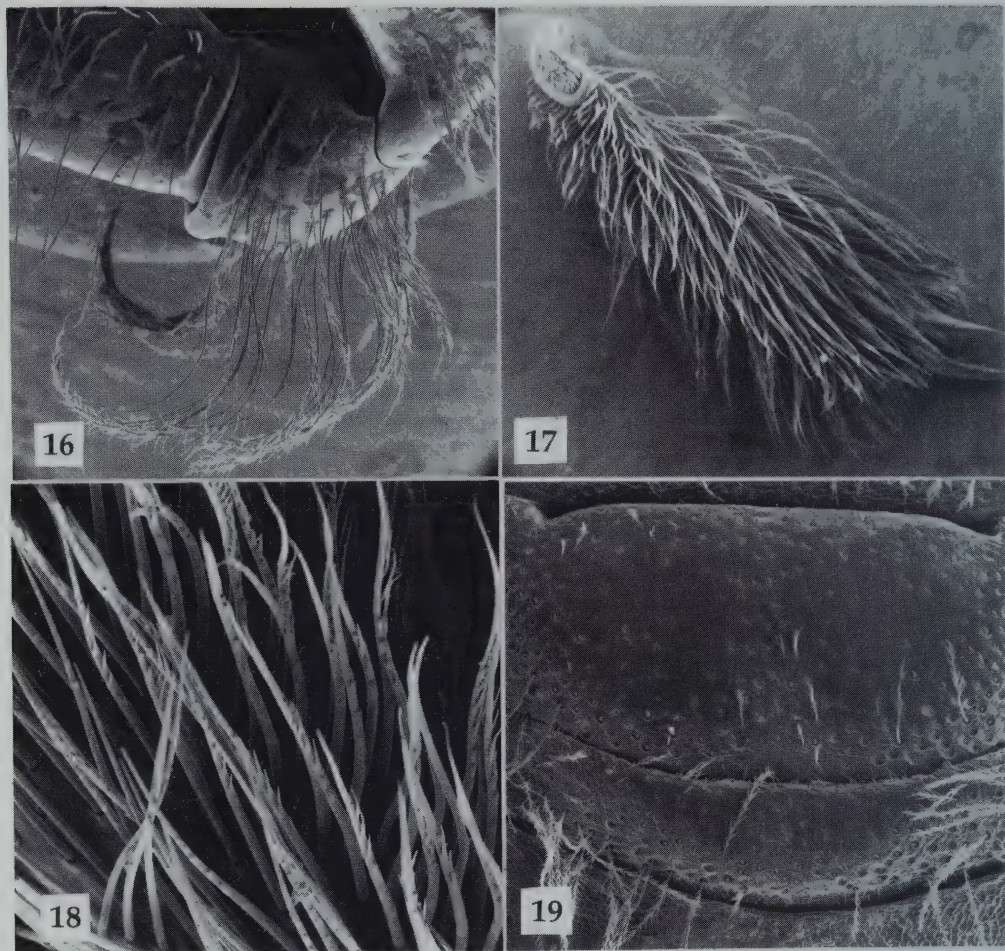
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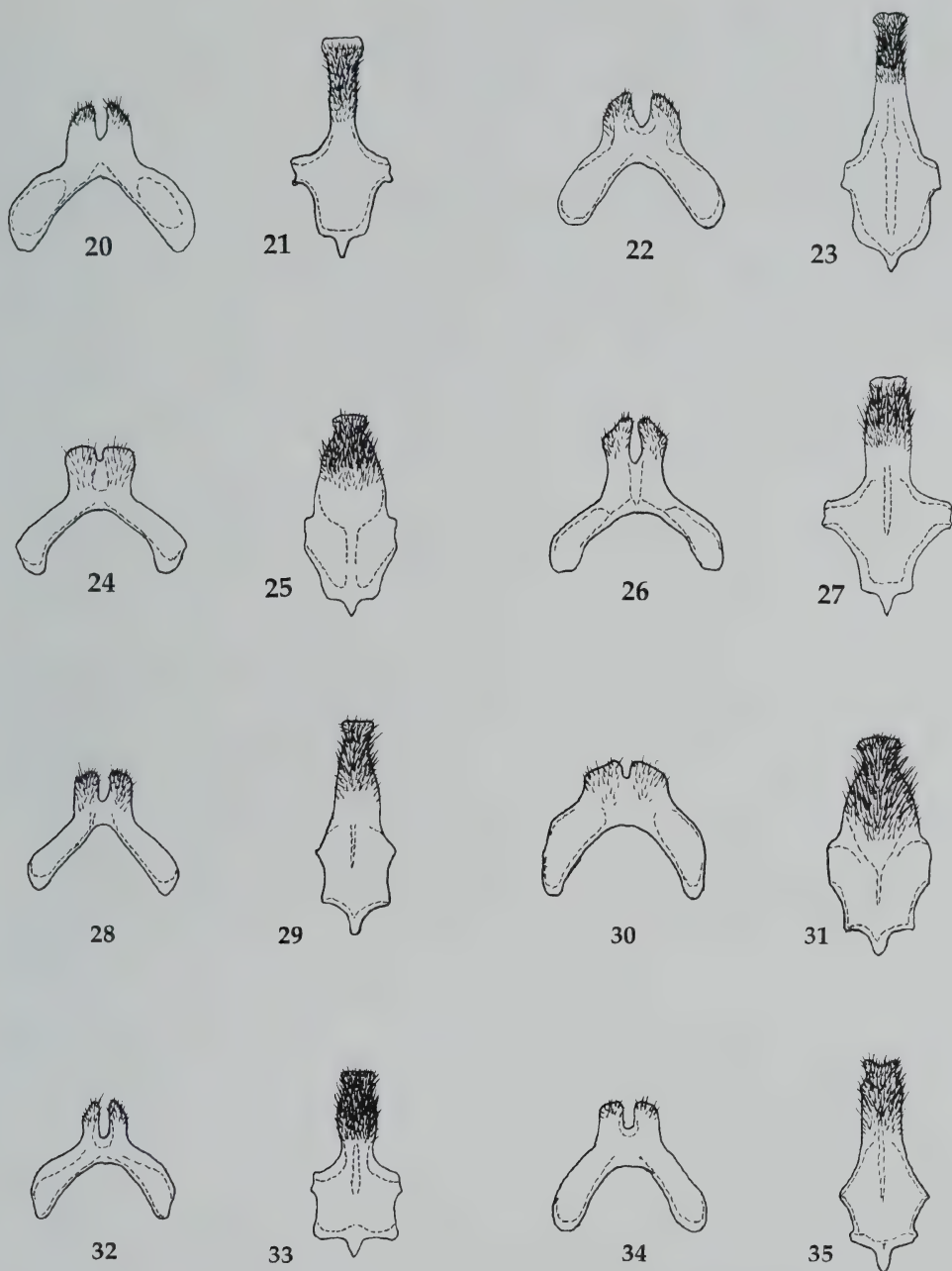


Figs. 10–15. *Andrena baeriae* Timberlake: 10—Male pronotum from above and slightly from anterior; note sharp dorsoventral ridge and rounded dorsolateral angle, X 70. 11—Male genital capsule, ventral view, X 30. 12—Male genital capsule, dorsal view, X 30. 13—Male sternum 7, X 100. 14—Male sternum 8, X 100. 15—Male tip of sternum 8, note flattened hairs as in Fig. 8, X 150.





Figs. 16–19. *Andrena leucomystax*, new species: 16—Female posterior hind leg showing trochanter and trochanteral flocculus, X 50. 17—Female right leg showing scopa, X 30. 18—Female showing scopal hairs enlarged, note weak plumosity, X 100. 19—Female scutellum and metascutum, dorsal aspect, X 70.



Figs. 20–35. Sterna 7 and 8 of males of species of *Andrena* subgenus *Hesperandrena*: 20–21—*A. escondida* Cockerall. 22–23—*A. pulverea* Viereck. 24–25—*A. duboisi* Viereck. 26–27—*A. lativentris* Timberlake. 28–29—*A. baeriae* Timberlake. 30–31—*A. leucomystax*, Thorp and LaBerge. 32–33—*A. dissona* Thorp and LaBerge. 34–35—*A. eremophila* Thorp and LaBerge.







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# Black-crowned Night-Herons of the Lake Calumet Region, Chicago, Illinois



## Article 3

### Nesting Ecology of Black-crowned Night-Herons at Lake Calumet Wetlands

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## Article 4

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## ABSTRACT

We examined the nesting ecology of a Black-crowned Night-Heron (*Nycticorax nycticorax*) colony located at wetlands associated with Lake Calumet in south Cook County, Illinois, during the 2002 and 2003 nesting seasons. This area of southeastern Chicago has been greatly impacted by heavy industry, solid and chemical waste disposal, urbanization, and altered hydrology.

Black-crowned Night-Herons (BCNH) have nested at five known locations at Lake Calumet wetlands during 1984–2003. Emergent cover (giant reed, *Phragmites australis*) was of primary importance to this colony for nesting during that time. Cottonwoods (*Populus deltoides*) also were used for nesting from the late 1980s to mid-1990s.

During 1993–2003 the herons began arriving at the colony as early as March 10. During the two years of this study the earliest indications of nest building and courtship occurred during the first week in April; the first pairs and precopulatory displays were observed during second week of April in both years. The egg-laying period extended from April 20 to June 12 in 2002, and from April 16 to May 27/28 in 2003. Hatching occurred from mid-May to the first few days of July in 2002, and from mid-May to June 19/20 in 2003. Juvenile dispersal in 2002 occurred from mid-July through late August, and from early July through mid-August in 2003.

Reproductive parameters in BCNH nesting at the north end of Indian Ridge Marsh (IRM), the primary nesting location for this colony in both years, were typical for this species. In 2002 the “recruitment” rate (number of young/nest surviving to 15 days) of 1.74 young/pair was below the threshold of 2.0–2.1 young/nesting pair thought to be necessary to maintain BCNH populations. However, recruitment increased to 2.22 young/pair in 2003, which was among the highest previously reported. The most important cause of nest failure was poorly constructed (flat) nests which allowed the eggs to roll out into the water. Although some eggs were lost to gulls and some hatched young were taken by unknown mammalian or avian predators, predation was not an important cause of nest losses at IRM.

## INTRODUCTION

The Calumet region of southwestern Lake Michigan was once a vast complex of glacial lakes, wetlands, and sand prairies. This region is now one of most heavily-industrialized in the U.S. and has been greatly impacted through industrial activities, waste disposal and discharge, urbanization, and changes to surface and groundwater hydrology. In spite of extensive habitat loss and degradation, the area remains among the most biologically diverse in the state of Illinois.

A number of wetland-dependent breeding birds of concern nest in marshes adjacent to Lake Calumet, including the state-endangered Black-crowned Night-Heron (*Nycticorax nycticorax*). One of the largest remaining breeding colonies in Illinois, this population is of considerable interest to resource professionals, environmental groups, and the conservation-minded public. Although BCNH populations have increased nationwide since banning of DDT and other persistent pesticides, Illinois has not enjoyed this recovery.

Young-of-the-year BCNH were reported in the Calumet marshes as early as 1874 (Nelson 1876–1877). Throughout much of the early part of the 20th century the Lake Calumet BCNH colony was located along the Calumet River just north of the confluence with the Grand Calumet River (Landing 1986). The BCNH have nested at wetlands adjacent to Lake Calumet since the Thomas J. O'Brien Lock and Dam went into operation in the late 1960s. The number of BCNH nesting at these wetlands has fluctuated widely over the last two decades. However, this population remained relatively stable at between 300 and 400 pairs during 1997–2003 (Marcisz et al. 2005).

Interest in the rehabilitation of these wetlands as part of the Calumet Open Space Reserve created the need for a better understanding of the ecology of this urban BCNH colony, in order to aid conservation planning and guide management activities. Accordingly, we examined the nesting ecology of BCNH at Lake Calumet's IRM during the 2002 and 2003 seasons.

## METHODS

### 2002

The activities of BCNH were observed for two-to-four-hour periods on eight occasions during April 5 to May 10 to document the timing of breeding activities. Nest building, pairing, breeding, and nesting behaviors were recorded. Nest monitoring was initiated at IRM on May 15, when 30 nests were marked by placing plastic flagging on *Phragmites* stems adjacent to each nest. The number of eggs and chicks was recorded for active nests. Additional nests were added May 20 ( $n=9$ ), May 26 ( $n=6$ ), May 30 ( $n=2$ ), and June 4 ( $n=1$ ). Nests were checked every four to seven days depending on weather and staff availability. The number and disposition of eggs (cracking, pipping, hatched, fell out, depredated, missing) and nestlings (present, missing, depredated) were recorded during each visit; eggs were numbered with a nontoxic marker. Twelve nests located in cottonwood trees at a colony located 13 km to the east at ISPAT Inland Steel (IIS), East Chicago, IN, were monitored for comparison; each monitored nest was numbered on a hand-drawn map of the site and observed from an elevated vantage point.

We conducted post-breeding surveys at IRM every two weeks during June–August 2002 to monitor the relative abundance of juvenile BCNH from about the time the first young became flighted through dispersal. These surveys consisted of walking an established transect adjacent to and the length of the colony at a slow pace, counting and aging the herons as the observer passed by them. To avoid double-counting, herons that took flight at the observer's approach and landed within an unsurveyed portion of the colony were not counted at that time.

### 2003

The activities of BCNH were observed for 1- to 2.5-hour periods on 11 occasions during April 9 to May 13. Nest building, pairing, breeding, and nesting behaviors were recorded. Nest monitoring at IRM was initiated on May 16; a total of 55 nests were marked ( $n=20$  on 5/16, 23 on 5/21, and 12 on 5/29). A total of 17 nests located at IIS were also monitored. Nest monitoring at IRM and IIS, respectively, was concluded July 10 and 23. Dates of first

known arrival of BCNH at Lake Calumet Wetlands (LCW) are based on periodic checks each spring of known previous nesting locations. Post-breeding surveys were initiated June 12 and concluded on August 21.

## RESULTS

### Nesting Habitat at Lake Calumet Wetlands 1984–2003

Throughout much of the early part of the 20th century, the Lake Calumet BCNH colony was located along the Calumet River just north of the confluence with the Grand Calumet River (Landing 1986). The construction of the Thomas J. O'Brien Lock and Dam resulted in the BCNH relocating to stand of eastern cottonwood (*Populus deltoides*) trees at Lake Calumet's Big Marsh (Fig. 1) during the early 1970s. The BCNH nested in the *Phragmites* at Big Marsh from 1984 through 1998; however, prolonged high-water levels in 1999 killed the *Phragmites* used for nesting structure. Although the emergent vegetation has recovered, as of 2003 the BCNH had not returned to nest at Big Marsh.

The cottonwoods at IRM were second in importance as a nesting site for this colony over the past 19 years (Table 1). The herons nested in the cottonwoods along the Calumet River at the southern portion of IRM during 1987–89; their abandonment of that rookery coincided with nesting by Red-tailed Hawks (*Buteo jamaicensis*) at that location in 1990. The BCNH began nesting at the cottonwood grove at IRM near 122<sup>nd</sup> St. in 1991, but have not nested at that site since 1996 after a pair of Red-tailed Hawks nested there. A lack of tree regeneration coupled with the death/poor condition of larger trees due to beaver (*Castor canadensis*) damage or high-water levels have been suggested as the causes for the failure of BCNH to return to nest in the cottonwoods. The *Phragmites* at the northern portion of IRM and at Heron Pond have become important nesting sites in recent years (Fig. 1).

During 2002 and 2003 the portion of IRM occupied by the nesting BCNH was characterized as a hemi-marsh condition, i.e., irregular-shaped and -sized stands of *Phragmites* interspersed with open water. The *Phragmites* cover ranged from narrow “fingers” and

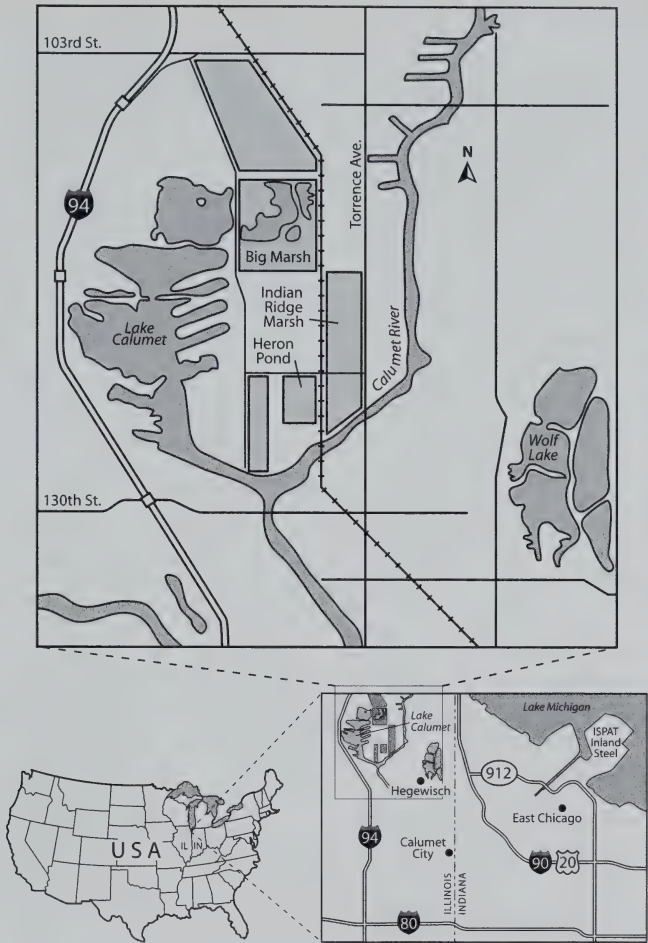


Figure 1. Map of southeastern Chicago, Illinois, and northwestern Indiana, showing locations used by nesting Black-crowned Night-Herons.

Table 1. Known Black-crowned Night-Heron nesting locations at Lake Calumet Wetlands, 1984–2003.

Location	Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Indian Ridge Marsh (IRM) <i>Phragmites</i>												X	X				X	X		X	X
IRM S. cottonwoods					X	X	X														
IRM N. cottonwoods									X	X	X	X	X								
Big Marsh <i>Phragmites</i>		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X					
Heron Pond <i>Phragmites</i>													X	X					X	X	



smaller isolated patches or clumps to larger blocks of cover. Thus, the area where the breeding colony was located was heterogenous with regard to available cover.

The BCNH colony was comprised of three "sub-colonies," each isolated from each other by an expanse of open water (Fig. 2). The northern subcolony held a greater proportion of the nests than either the eastern or southern subcolonies. Isolation of nesting areas from the shoreline by deeper water and thick emergent cover may have reduced the incidence of mammalian predation and vandalism/disturbance. Least isolated from shoreline by distance or deep, open water, nests in the eastern subcolony did experience greater predation loss in 2002 than in the monitored portion of northern subcolony.

The BCNH constructed nests of the previous year's *Phragmites* stems (occasionally lined with purple loosestrife (*Lythrum salicaria*) or unidentified woody stems) placed within a clump of standing stems. Nest distribution was generally clumped. There were concentrations of nests in close proximity (some less than a meter apart), generally in areas of sparser cover (i.e., near edges of cover or where *Phragmites* stems were less dense). Occasional nests were located in single clumps of reeds or scattered in denser cover.

### Arrival and Courtship

The earliest date that BCNH have been observed at LCW during the period 1993 to 2003 was on March 10, 1994 (Table 2). During 1993, 1994, 1995, 2000, 2001, and 2003 no herons were observed on earlier (i.e., prior to date first observed) visits; no previous visits were recorded for 1996, 1997, 1998, and 2002. No BCNH were observed on March 29, 1992 or March 23, 1999, thus the herons apparently began arriving after those dates. Although we cannot be sure of the exact date of arrival based on these data, they do indicate that BCNH typically began arriving in substantial numbers during the latter half of March.

BCNH may continue to arrive at LCW well after others have begun nest building and pairing. In 2002 the number of BCNH at IRM greatly increased between April 26 and May 12. Also, no BCNH were observed at nearby Heron Pond (HP) until April 6 of that year. Similarly, BCNH were present at IRM as early as March 10 in 1994, but were not observed at

nearby Big Marsh (BM) as late as May 1, though were known to be successfully nesting there later in the season.

In 2002 BCNH were first observed at LCW on March 17, and were initially seen ( $n=4$ ) carrying sticks on April 6. Early in the breeding cycle this behavior signifies beginning of nest building by males just prior to courtship and accepting a female at the nest (Meyerriecks 1960, Palmer 1962). Later, after pair formation, the male will present twigs to females prior to copulation and this behavior persists until after the eggs are laid. Gross (1923) reported that the first eggs were laid an average of seven days after start of nest construction; based on this information the first eggs would have appeared at LCW around April 13.

The first pairs were observed at nests at IRM on April 16; the number of pairs seen from an unobstructed vantage point increased from 2 on April 16, to 10 April 23, and 22 on May 2. Circling flights (synchronization of sexual behavior in early pair formation, Meyerriecks 1960) were observed on April 16; precopulatory displays (including billing, feather nibbling, twig presentation, erection of feathers, and neck stretch), and copulation were recorded as early as April 18 and April 19. According to Allen and Mangels (1940) the first eggs are laid an average of 3.3 days after copulation or 4–5 days after pair formation. Based on this information the first eggs would have appeared on April 20 or 21.

In 2003 BCNH were first observed carrying sticks on April 9, thus the first eggs would have appeared at LCW around April 16; in fact, pairs were first observed at nests on April 16. Precopulatory displays (including billing, feather nibbling, twig presentation, erection of feathers, and neck stretch) were recorded as early as April 18, thus the first eggs would be expected to have appeared on April 21. Based on our sample of nests, the first clutches were initiated on April 16, with half the nests initiated by May 8, and the last on May 23.

### Nesting Phenology

The phenology of BCNH clutch initiation, egg hatching, and juvenile fledging/dispersal at IRM was reconstructed based on direct observation (i.e., nest monitoring) and the following assumptions:

BCNH Nesting Colonies (2002–2003)  
Lake Calumet Area



Figure. 2. Location of Black-crowned Night-Heron colony in *Phragmites* cover at Indian Ridge Marsh during 2002 and 2003 and Heron Pond in 2002.

Table 2. Number at first sighting by week of occurrence of Black-crowned Night Herons at Lake Calumet Wetlands, 1993–2003.

Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Week											
March 1–7							No Data				
March 8–14		1									
March 15–21										16	
March 22–28			14		40	3		2			18
March 29–April 4	25			17					75		

- 1) approximately two days to lay each egg (Gross 1923, Palmer 1962, Tremblay and Ellison 1980);
- 2) an average incubation period of 24 (23.5) days for A-eggs (i.e., first egg laid; Custer et al. 1992);
- 3) hatching one day after pipping, two days after cracking (Custer and Peterson 1991);
- 4) B-egg hatches about one day after A-, and C- hatches two days after B- (Custer et al. 1992); we assumed D-egg hatched one day after the C-egg;
- 5) flight is attained at about six weeks (42 days) of age (Palmer 1962, Wolford and Boag 1971);
- 6) on average, young of the year disperse at 58 days of age (Erwin et al. 1996).

In 2002 we initially marked 30 nests on May 15 and added new nests as encountered in that portion of the colony (n= 9 on May 20, n= 6 on May 26, n= 2 on May 30, and n= 1 on June 4). Based on our monitored sample of nests, we estimated that clutches were initiated as early as April 20, with half being initiated by mid-May, and the last on June 7 (Fig. 3). The last clutches initiated were in recycled nests; excluding second and third clutches (i.e., recycled nests) the latest a clutch was initiated, based on our marked sample, was May 23.

The estimate of April 20 for the initiation of laying coincides with estimates of clutch initiation based on our observations of pre-copulatory displays and copulation and information provided in Allen and Mangels (1940).

The first eggs would have hatched by mid-May, with A-eggs from half of the monitored nests hatching by the second week in June; A-eggs from the last nests initiated would have hatched on July 1 (Fig. 3). Thus, eggs would have been present at IRM over a period of about two and one-half months (April 20 to July 4-5).

Based on a flightless period of six weeks (Palmer 1962), the first and last young, respectively, attained flight on June 25 and August 10 (Fig. 3). Erwin et al. (1996) reported that age of dispersal in BCNH averaged 55 and 60 days in the two years of their study. Thus, based on an average dispersal age of 58 days, dispersal of juvenile IRM BCNH began about mid-July and continued through late August, with most having reached dispersal age by the middle of August. This coincides well with the results of our post-breeding surveys, which revealed a precipitous decline in juveniles observed at IRM between August 10 and 24 (see Fledging and Dispersal below).

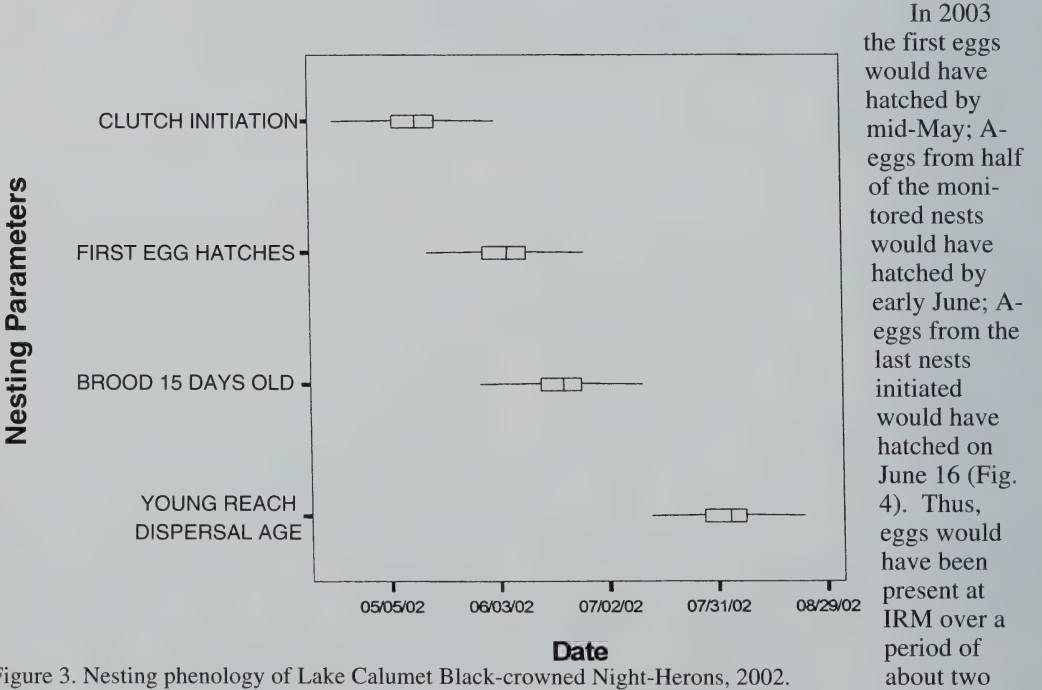


Figure 3. Nesting phenology of Lake Calumet Black-crowned Night-Herons, 2002.



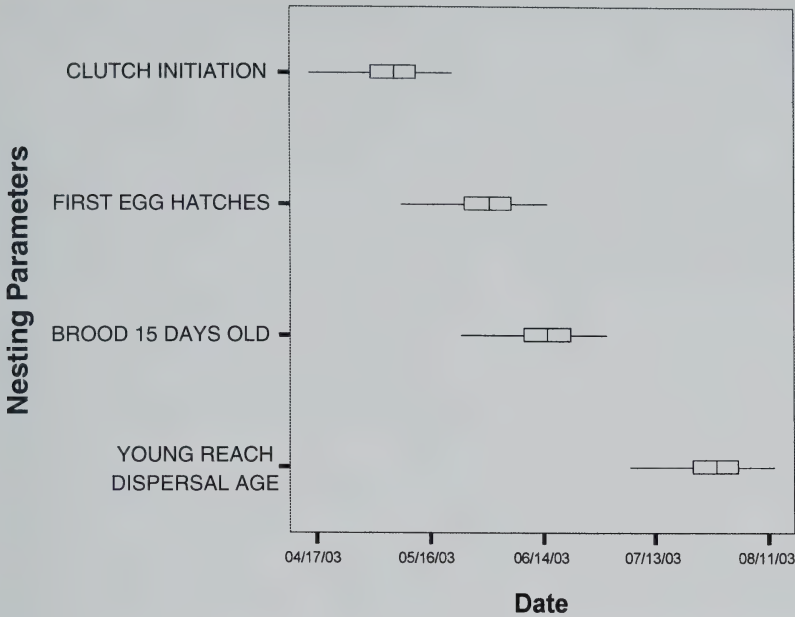


Figure 4. Nesting phenology of Lake Calumet Black-crowned Night-Herons, 2003.

months. The first young attained flight on July 5, and dispersal of juvenile BCNH from IRM began the first week in July and continued through mid-August, with most having reached dispersal age by the end of July. This coincides well with the results of our post-breeding surveys which revealed that most juveniles had left by mid-August of that year (see Fledging and Dispersal below).

**Clutch Size**

Mean clutch size (all clutches) of BCNH nesting at IRM in 2002 was similar to that of clutches in tree nests at nearby ISPAT Inland Steel (IIS) (Table 3). Mean clutch sizes (all clutches) at IRM in 2002 and 2003 were very similar; clutch size declined considerably at IIS in 2003.

A total of six monitored nests at IRM was recycled (one nest with second and third clutches) in 2002. Mean clutch size for initial clutches was slightly higher than for all clutches (Table 3). We did not document any recycled nests at IRM in 2003.

When sorted by median date of initiation (5/13, see Nesting Phenology above), i.e., early nests < median date, late nests > median date, the average clutch size in 2002 was 0.48 eggs larger in nests initiated on or prior to the median date. Thus, early clutches were nearly

complete; in the other two nests, one or more of the original eggs were found in the water and new eggs added to the nest. In one of these, a known total of five eggs were laid. In the other, the nest was recycled following the disappearance of the original clutch of three eggs. At least six eggs were subsequently found in the nest, with all eventually disappearing; four eggs (some from both clutches) were found in the water below this nest. We did not identify any such “dump nests” at IRM in 2003.

**Nest, Egg, and Nesting Fate**

The most common cause of failed clutches at IRM in 2002 was through poorly constructed nests, which allowed eggs to roll out into the water (Table 4). Predation was the next most common cause of nest failure; the complete disappearance of two clutches/broods may also have represented predation events. Including these, 7 of 51 (13.7%; includes second clutches) monitored clutches/broods were lost to predation at IRM. This amounted to the loss of 13 eggs and 7 chicks; coupled with 2 eggs with bill marks found in completed clutches, a minimum of 22 eggs or nestlings were lost to nest predators. It was difficult to determine the cause of death of most nestlings due to condition of carcasses upon discovery. BCNH

16% larger than late clutches; however, we did not detect this difference statistically ( $t_{28}=1.8$ ,  $P=0.08$ ).

At least four nests at IRM in 2002 had additional eggs laid in them after the original clutches were complete (based on the time interval between last egg of the clutch laid and presence of new eggs). In two cases one additional egg was laid after clutches of three were

Table 3. Clutch size for Black-crowned Night-Herons nesting at Indian Ridge Marsh (IRM) and Inland Steel, 2002 and 2003, and as reported in previous studies.							
Location/Status	n	Mean	S.E.	Min-Max	Mode	Comments	Citation
IRM 2002 — all clutches 2002	40	3.40	0.11	2-5	3	includes second clutches; nearly bimodal (3- and 4-egg clutches)	this study
IRM 2002 — first clutches only	36	3.42	0.12	2-5	3/4	excluding second clutches; bimodal	this study
IRM 2002 — first clutches ≤ May 13	18	3.56	0.17	2–5	4	initiated prior to or on median date; nearly bimodal (3- and 4-egg clutches)	this study
IRM 2003 — all clutches		3.36					this study
IRM 2002- first clutches > May 13	17	3.08	0.19	2–4	3	initiated after median date	this study
ISPAT Inland Steel, IN 2002 — first clutches	13	3.38	0.21	3–5	3	tree nests; exposure to environmental contaminants likely	this study
ISPAT Inland Steel, IN 2003		3.06				tree nests; exposure to environmental contaminants likely	this study
Maryland	69	3.46	NA	2–5	4	nearly bimodal (3- & 4-egg clutches); shrub/tree nests; no apparent impact environmental contaminants	Rattner et al. 2001
Oregon and Washington — all clutches	260	3.45 <sup>1,2</sup>	0.08–0.11	2–5	NA	means 3.10 to 3.92; shrub/tree nests; no apparent impact environmental contaminants	Blus et al. 1997
Oregon and Washington — first clutches	208	3.47 <sup>1,2</sup>	0.08–0.12	2–5	NA	means 3.09 to 3.93; shrub/tree nests; no apparent impact environmental contaminants	Blus et al. 1997
Idaho	281	3.6 <sup>1,2</sup>	0.08–0.13	1–6	3/4 <sup>2</sup>	means 3.4 to 3.7; shrub/trees; DDE impacts on reproduction	Findholt and Trost 1985
NV, OR, WA — ≤ 8 ppm DDE	133	3.75 <sup>1,2,3</sup>	0.15 <sup>1</sup>	NA	NA	means 3.67 to 3.80; shrub/tree nests; no apparent impacts environmental contamination	Henny et al. 1984
NV, OR, WA — > 8 ppm DDE	50	3.17 <sup>1,2,3</sup>	0.19 <sup>1</sup>	NA	NA	means 3.00 to 3.41; shrub/tree nests; DDE impacts on reproduction	Henny et al. 1984
Massachusetts and Rhode Island	346	3.79 <sup>1,2,3</sup>	NA	2–5	4	means 3.66 to 3.96; possible DDE impacts on reproduction	Custer et al. 1983
North Carolina	121	3.32 <sup>1,2,3</sup>	NA	2–5	3	means 3.08 to 3.50; no apparent impacts environmental contaminants	Custer et al. 1983
Quebec	98	4.1 <sup>1,2,3</sup>	0.1	1–6	NA	means 3.9 to 4.2; shrub/tree nests; no apparent impacts environmental contaminants	Tremblay and Ellison 1980
Alberta — first clutches	116	3.60 <sup>1,2,3</sup>	NA	1–6	3/4 <sup>2,3</sup>	means 3.2 and 4.0; emergent vegetation nests	Wolford and Boag 1971
CA — pre-1947	35	3.86	NA	NA	NA	unknown status	(see Henny et al. 1984)
NV, OR, WA — pre-1947	41	3.80 <sup>1,2,3</sup>	NA	2–5	NA	unknown status	Henny et al. 1984
Utah — pre-1947	41	4.1	0.13	2–6	4	unknown status	Findholt and Trost 1985

<sup>1</sup> Grand mean; <sup>2</sup> Multiple colonies; <sup>3</sup> Multiple years

Table 4. Fate of Black-crowned Night-Heron Clutches/Broods at Indian Ridge Marsh, Cook County, Illinois, 2002.		
Fate of Clutch	Number of Clutches	Percent of Clutches
Successful <sup>1</sup>	34	66.7
Eggs Rolled Out, Poorly Constructed Nest	7	13.7
Depredated <sup>2</sup>	5	9.8
Abandoned <sup>3</sup>	3	5.9
Eggs/Nestlings Gone, No Signs	2	3.9

<sup>1</sup> at least one nestling survived to 15 days post hatch

<sup>2</sup> one clutch assumed abandoned after one egg depredated

<sup>3</sup> one damaged egg abandoned

Notes-

a) another 4 broods known to completely fail after 15 days

b) determined minimum 6 predation events (clutch/brood or single eggs/chicks)

c) 11 chicks dead in nest= 3 depredated (same nest), 8 unknown fate

eggs hatch asynchronously and later-hatching nestlings may be disadvantaged, with competition by older siblings leading to starvation, drowning, or trampling of younger nestlings. This was undoubtedly the cause of the disappearance of many nestlings. We frequently visited nests with two or three thriving siblings, and the smaller, less thrifty individual was often missing at our next visit.

Several eggs had apparently been depredated by Ring-billed Gulls (RBG), judging by bill marks, although in at least one case the gulls may have scavenged a previously abandoned clutch. Large numbers of RBG frequented the area and were often seen fishing in open-water portions of IRM. We did not observe Gulls at BCNH nests, although we did note a BCNH briefly chase a RBG that was flying low over the colony. We did find and examined three siblings < 5 days old that had been killed by single pecks to the back of their skull.

Most nests successfully fledged at least one young on 2003 (Table 5); there were no known or suspected losses of entire clutches or broods to predation. Although no eggs were observed in water, all eggs missing from two flat-topped nests were assumed to have rolled out into the water. One nest was presumed abandoned as the marked eggs were present well after they should have hatched. At least 25 eggs were missing or otherwise failed to hatch. Twenty-three nestlings did not survive to fledging (i.e., 15 days post-hatch); of these, 21 were missing, 1 was found dead in nest (cause unknown), another had fallen out of the nest and was found with its neck caught between *Phragmites* stems.

### Fledging and Dispersal

The number of juveniles observed in 2002 increased dramatically between mid-July and mid-August. The first appearance of juveniles between June 29 and July 13 coincides rather well with our first observation of flighted juveniles on July 3 while performing nest checks, and estimated dates that older chicks attained flight. The number of juveniles observed peaked on August 10, before declining precipitously between August 10 and 24 (Fig. 5). This reduction in juveniles is consistent with our expectation, based on nesting phenology (see above), that 97% of juveniles would have reached dispersal age (~58 days

post-hatch) by August 24. In 2003 the number of juveniles observed peaked earlier than in 2002; in 2003 most young were gone from IRM by mid-August (Fig. 5).

### Productivity

While comparisons of productivity between studies are useful, the ratio of breeders to non-breeders, food availability, local weather patterns, climate/growing season (latitude), predation, and a variety of density-dependent factors can influence productivity. Most powerful are comparisons with contemporary local/regional populations. The only sizable colony in the south Chicago area available to us for comparison during 2002 and 2003 was at IIS, located on the Lake Michigan shoreline only 15 km from the Lake Calumet colony (Fig. 1). This colony is located at the same latitude as LCW; the IIS BCNH nested in cottonwood trees during this study.

Daily nest survival rate was similar between the colonies we examined (Table 6). In 2002 clutches at IRM and IIS had a lower likelihood of surviving the incubation period, when compared to 2003 when the survival rate of nests to hatch was relatively high at both locations.

Daily survival rate of nests during the nestling period was similar between the IRM and IIS colonies (Table 6). Survival of broods to 15 days of age was lower at IIS than at IRM; brood survival at IRM was similar between years.

In 2002, nest success (a function of survival rate to hatching and survival rate to fledging) at IRM was greater than at IIS, which was poor (Table 6). Nest success at both IRM and IIS improved between 2002 and 2003, although remained poor at the latter.

Egg success, the probability of an egg hatching, was low at IIS during 2002, though improved between 2002 and 2003 at this site and at IRM. Nestling survival was low at IIS in 2002; survival of young to 15 days improved at both IRM and IIS between years (Table 6).

The mean number of young surviving/nest was very low at IIS, whereas "recruitment" was relatively high at IRM by comparison (Table 6). Recruitment increased at both IRM and IIS between 2002 and 2003.



Table 5. Fate of Black-crowned Night-Heron Clutches/Broods at Indian Ridge Marsh, Cook County, Illinois, 2003.		
Fate of Clutch	Number of Clutches	Percent of Clutches
Successful <sup>1</sup>	52	94.5
Eggs Rolled Out, Poorly Constructed Nest	2	3.6
Depredated	0	0
Abandoned	1	1.8
Eggs/Nestlings Gone, No Signs	0	0

<sup>1</sup> at least one nestling survived to 15 days post-hatch

<sup>2</sup> no confirmed or suspected predation of marked nests

Notes-  
a) 23 chicks failed to survive 15 days= 21 missing, 2 chicks dead in nest (1 accidental death, 1 unknown cause of mortality)

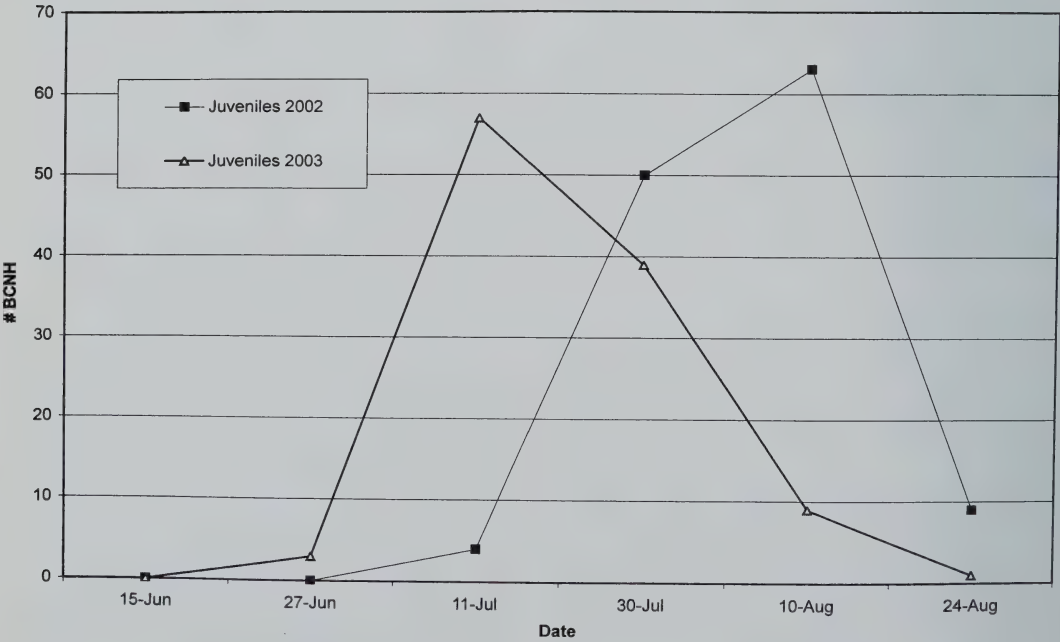


Figure 5. Numbers of juvenile Black-crowned Night-Herons observed at Indian Ridge Marsh colony during 2002 and 2003 post-breeding surveys.

Table 6. Reproductive parameters in a Black-crowned Night-Heron colony located in the Calumet region of Illinois and northwestern Indiana, 2002 and 2003.

Location	Indian Ridge Marsh—This Study 2002	Inland Steel —This Study 2002	Indian Ridge Marsh—This Study 2003	Inland Steel —This Study 2003	Maryland —Rattner et al. 2001	Pacific Northwest —Blus et al. 1997	San Francisco Bay —Hothorn et al. 1995	East Coast —Custer et al. 1983
Nesting Parameters								
Egg Laying and Incubation (n)	46	15	55	17	69		485	531
Daily Survival Rate	0.9895	0.9855	0.9985	0.9931	0.9936	0.9240–0.9934 <sup>4</sup>		
Survival Rate to Hatch	0.7762 <sup>1</sup>	0.7043 <sup>1</sup>	0.9635	0.8474	0.8517 <sup>2</sup>		0.475–0.701	0.547–0.902 <sup>2</sup>
Nesting Period (n)	37	13	52	15	59		395	(<531?)
Daily Survival Rate	0.9922	0.9864	0.9899	0.9809	0.9911	0.9782–1.000 <sup>5</sup>		
Survival Rate to Fledging	0.8892 <sup>3</sup>	0.6245 <sup>3</sup>	0.8593	0.7485	0.8745 <sup>3</sup>		0.691–0.896	0.758–1.000 <sup>3</sup>
Nest Success	0.6920	0.4398	0.8280	0.6343	0.7448			0.530–0.867
Probability of Egg Hatching	0.8860	0.6852	0.9195	0.8333	0.8933			0.852–0.917
Probability Young Survived 15 days	0.8365	0.5143	0.8688	0.7714	0.8917			0.771–1.000
Egg Success	0.5115	0.1550	0.6614	0.4078	0.5932			0.385–0.716
Mean Clutch Size	3.40	3.38	3.36	3.12	3.46			3.08–3.96
Mean Number of Young Surviving 15 Days	1.74/nest	0.52/nest	2.22/nest	1.27/nest	2.05/nest	0.41–1.83/nest	1.45–2.04/nest	1.19–2.65

<sup>1</sup>= 24 day laying and incubation period; <sup>2</sup>= 25 day laying and incubation period; <sup>3</sup>= 15 days post-hatch; <sup>4</sup>= 27 day laying and incubation period; <sup>5</sup>= 14 days post hatch

## DISCUSSION

BCNH utilize a wide range of arboreal habitats for nesting including upland orchards (Gross 1923), bottomland forests (Bjorklund and Holm 1997), coastal islands (Parsons 1995), and trees in towns and cities (Farwell 1919, Cunningham 1945). Breeding colonies are also frequently located in emergent vegetation such as *Phragmites* or cattails (*Typha*), with nests located just inches above the water (Nelson 1876–1877, Rockwell 1910, Greenwood 1981). During the 20 years from 1984 to 2003 the Lake Calumet BCNH changed nesting locations as habitat conditions dictated, i.e., when nesting cover was impacted by fire, flooding, or succession (or lack thereof). The colony has maintained a high degree of fidelity to this area in spite of these changes. This supports Graber et al.'s (1978) assertion that the quality of the surrounding foraging habitat is a more important criterion for nesting than the particular habitat in which the nests are actually placed.

There appeared to be a clear preference for relatively open nest sites (i.e., of lower *Phragmites* stem density). A more open nest would seem to result in greater nest predation risk. However, 1) nests tended to be clumped in these more open areas and there may be higher survival of individual nests within groups, and 2) there may be greater inclusive fitness in that parents may be better able to avoid predators at some risk of clutch/brood predation.

Clutch size may be affected by a variety of factors linked to female condition and/or environmental quality (Winkler and Allen 1996). Mean clutch size in our study in 2002 was similar to that of recently-studied colonies in Maryland and the Pacific Northwest. The average clutch size at IRM was at the upper end of the range of average clutch sizes observed in colonies that were thought to be impacted by DDE, and below the range of clutch sizes observed for “clean” colonies in the United States and Canada. Interestingly, mean clutch size for first and second clutches in our study differed by the same amount as those in colonies in Oregon and Washington. The reason for the decline in clutch size between 2002 and 2003 at IIS was unknown.

Early clutches (< median date) were larger, as compared with those completed later (> median date). Custer et al. (1983) noted that BCNH clutches initiated later in the

season had a larger proportion of smaller clutches (i.e., < four eggs) than earlier clutches. It is unclear as to whether such seasonal declines in clutch size are related directly to female condition or an adaptive response to declining resources as nesting season progresses (Winkler and Allen 1996).

Our estimate of April 20 to June 10 for the egg-laying period at IRM in 2002 is similar to April 24 to June 18 reported by Graber et al. (1978) for northern Illinois colonies. However, our estimate of April 20 to May 26 for the egg-laying period in 2003 is somewhat shorter than reported by Graber et al. (1978). In 2002, eggs would have been present at IRM over a period of two and one-half months; this is a longer egg period than in 2003 by about two weeks. This is consistent with the number of juveniles present during our post-breeding surveys; most young were gone from IRM by mid-August of that year, or about two weeks earlier than in 2002. We did not encounter recycled nests in 2003, thus there may have been fewer renesting attempts in that year.

Daily survival rate of nests at IRM and IIS during the nestling period were similar to those examined by others. Survival of broods to 15 days of age was lower in tree-nesting BCNH at IIS than the *Phragmites*-nesting colony at IRM or reported in previous studies. Parsons (1995) reported that nestling survival was lower in Cattle Egrets nesting in shrubs as compared to those nesting in *Phragmites* in the same colony (Parsons 1995). We sometimes noted eggs and carcasses of young on the ground below nesting trees at IIS. This colony was directly exposed to winds off of Lake Michigan, and we assume that some of this loss may have been due to high winds and other mishaps causing nestlings to fall out of trees. Brood survival at IRM was similar between years, and was relatively high in comparison with past studies.

Although some eggs and young were lost to predation, we were not able to determine the cause of all losses. It is plausible that RBG were responsible for the disappearance of some of the eggs and smaller nestlings that weren't accounted for. However, predation by this species did not seem to be an important factor at IRM, particularly in light of the large numbers of RBG frequenting this wetland. In contrast, RBG were responsible for the poor productivity of some BCNH colonies in Alberta (Wolford and Boag 1971). Predation by Common Ravens (*Corvus corax*) essentially eliminated production in one colony in the



western United States (Henny et al. 1984), and egg depredation by American Crows (*Corvus brachyrhynchos*) affected nest success in some colonies in the Pacific Northwest (Blus et al. 1997). Although gulls, crows, and other avian predators were present, predation did not have a demonstrable impact on productivity of the LCW BCNH colony.

Henny (1972) determined that 2.0–2.1 young produced/breeding pair is needed to maintain BCNH populations, and Wolford and Boag (1971) calculated that a colony producing 1.1 fledged young/pair would disappear in 20 years. Thus, the estimated fledging rates (actually survival to 15 days) at IRM in 2002 in this study may not have been high enough to maintain a stable population. However, recruitment in 2003 was among the highest reported in other studies. It is not unusual for productivity of BCNH colonies to vary between years. For example, Greenwood (1981) reported annual production of 0.23, 0.57, and 2.20 fledglings/pair for a colony occupying a marsh in North Dakota; strong storms with hail and high winds were responsible for large losses of nests and young in two of those years. However, in the absence of such catastrophic events (including heavy losses to predation) productivity of BCNH does not vary this dramatically between years (e.g., see Custer et al. 1983).

Exposure to environmental contaminants has been associated with impaired reproduction (Custer et al. 1983, McEwen et al. 1984, Henny et al. 1984, Findholt and Trost 1985, Hoffman et al. 1993, Hothem et al. 1995) and teratogenic effects (Hoffman et al. 1993, Hothem et al. 1995) in BCNH. At the time of this writing we are examining selected environmental contaminants and biomarkers of exposure in pipping embryos collected from this colony in 2002; the results of this work are not addressed here. However, we did not observe any gross deformities in pipping embryos or nestlings and, as noted above, reproductive parameters for BCNH nesting at IRM were within normal limits for this species. Thus, it would appear that environmental contaminants are not having observable impacts on the productivity of this population.

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ILLINOIS  
NATURAL  
HISTORY  
SURVEY

Black-crowned Night-Herons  
of the Lake Calumet Region,  
Chicago, Illinois



Article 4

Population Trends in a Black-crowned  
Night-Heron Colony at Lake Calumet  
Wetlands

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## ABSTRACT

The number of active Black-crowned Night-Heron (*Nycticorax nycticorax*) nesting colonies in Illinois has declined significantly over the past century. Habitat loss/degradation and other factors such as exposure to environmental contaminants and competition for nest sites at established colonies may have contributed to this decline. In this study, we examined recent trends in population levels of Black-crowned Night-Herons nesting at wetlands associated with Lake Calumet in southeastern Chicago, Illinois. The number of Black-crowned Night-Herons nesting annually at these wetlands has fluctuated widely over the last two decades. Immigration of herons from riverine colonies may have driven population increases during the mid-1980s and early 1990s. However, this population has remained relatively stable at between 300 and 400 pairs during 1997–2003.

## INTRODUCTION

The decline of the colonial-nesting Black-crowned Night-Heron (*Nycticorax nycticorax*) (BCNH) as a breeding species in the state of Illinois has been documented by a number of authors. According to Bohlen (1989:16), “The Black-crowned, like other heron species, is declining in numbers and has been for the past half-century.” Mlodinow (1984:76) reported that, in the Chicago area, “[BCNH] Nesting colonies are steadily becoming smaller and fewer...” And Graber, et al. (1978:54) indicated that their Illinois data suggested “a serious decline in the BCNH population in the past half-century.” Results of the Illinois Colonial Waterbird Survey indicated that there were an estimated 1,900 nesting pairs in 1987 (Kleen 1987), compared with 400+ in 1999 (Kleen 1999).

Young-of-the-year BCNH were reported in the Calumet marshes as early as 1874 (Nelson 1876–1877). Although there are no accurate figures for the extent of these wetlands during presettlement times, historic maps suggest that marshland formations totaled at least 22,000 acres on the Illinois side of the state line. Due to the impacts of industry, railroads, waste disposal, urbanization, and hydrologic changes during the 20th century, only approximately 500 acres of wetlands remained at Lake Calumet (LCW) in recent

years (Landing 1986), much of it in an impaired state. Despite these habitat losses and degradation, BCNH have maintained a tradition of nesting at wetlands associated with LCW in southeastern Chicago (Fig.1). The common reed (*Phragmites australis*) has been of primary importance as nesting cover for this colony since 1984; cottonwood trees (*Populus deltoides*) were of secondary importance in some years.

We present the results of weekly population censuses conducted during spring of 2002 and 2003 of BCNH nesting at LCW, along with a compilation of the results of censuses of nests and/or breeding BCNH conducted since 1984.

## METHODS

**Population Levels**—BCNH are largely crepuscular/nocturnal foragers that disperse from their daytime roosts/nesting areas at dusk. During the 2002 and 2003 breeding seasons, BCNH population censuses were conducted at dusk at the northern portion of Indian Ridge Marsh on a weekly basis from the arrival of the BCNH in late March through late May (the final census in 2003 was conducted on June 1). Censuses were conducted under conditions of no precipitation and winds < 15 mph by two observers beginning one hour before sunset and continuing until the rate of departure was < 2 herons/5 minute period. As days lengthened the herons became active earlier and as of May 1 censuses were initiated two hours before sunset.

Although no BCNH were noted at nearby Heron Pond on March 24 and 30, 2002, a number of herons were observed at this site on April 6, 2002. After mid-April 2002 it became apparent that some herons were nesting at Heron Pond and censuses were subsequently conducted on April 26 and May 12, 2002 at that site. Early in the spring of 2003, a wildfire at Heron Pond destroyed essentially all of the emergent vegetation at that site, eliminating the BCNH's nesting substrate for the season. No BCNH nesting occurred at Heron Pond that year.

**Peak Numbers**—Peak numbers of BCNH were based on evening censuses of BCNH leaving nesting colonies to forage, conducted during 1992–2003. Data for 1992–2001

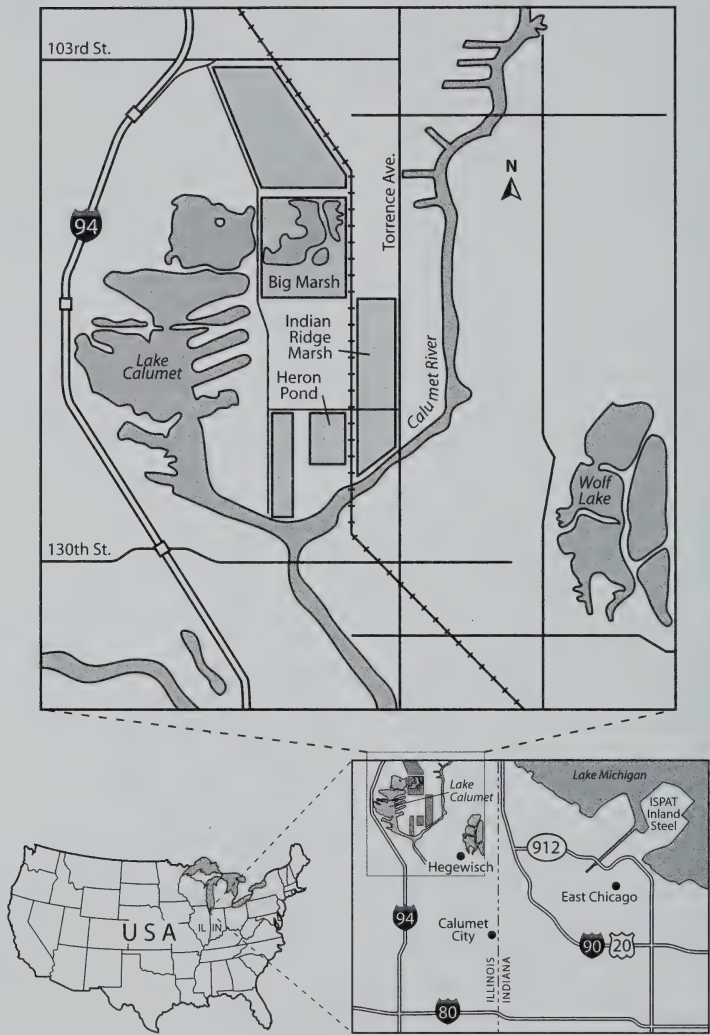


Figure. 1. Map of southeastern Chicago, Illinois, and northwestern Indiana, showing locations used by nesting Black-crowned Night-Herons.



represented an average of 2 to 3 counts conducted during late-April/early-May of each year; the 2002 data represented the maximum of 11 counts conducted March 24 to May 26; the 2003 data represented the maximum of 11 counts conducted from March 23 to June 1. These were combined with counts of occupied tree nests (multiplied by 2 BCNH) conducted during 1987–89 and 1991–95.

**Number of Nests**—The number of nests for each year were calculated from actual nest counts conducted during 1984–91, combined with estimates of nesting pairs for the years 1992–2003. We compiled the results of annual nest counts conducted at Big Marsh during mid- to late-May of 1984–91 (no data for 1990). These counts consisted of a line of five to seven observers walking transects through the *Phragmites* stands and counting nests seen to one side of each person. A portion of the colony was not surveyed in 1986 and 1987; it was estimated that <15% of the nesting colony was missed, thus we added 15% to the nest counts in those years. Direct counts of tree nests located at Indian Ridge Marsh during 1987–91 were added to these counts. The number of nests present during 1992–2003 were estimated by dividing peak counts of BCNH by two to represent a pair for each nest. We feel that this provides a reasonably accurate approximation of breeding pairs (nests) as: 1) our data suggests that prior to incubation the vast majority of BCNH are counted during evening censuses, 2) 99.3% of known-aged herons observed during our evening population censuses were >1 year old, and 3) there are numerous accounts of nesting by one-year-old BCNH (Gross 1923, Nobel and Wurm 1942, Custer and Davis 1982). In 1994 the herons began nesting at nearby Big Marsh (in addition to the *Phragmites* and cottonwoods at Indian Ridge Marsh) late in the season. Thus, a complete count was not conducted at that location. Consequently, the 1994 estimate of 410 nests represents a minimum and was not included in Figure 4.

## RESULTS

In 2002, BCNH were first noted at LCW on March 17; numbers gradually increased from the start of the evening population censuses on March 24 through May 12, when they peaked

at 750 herons (Fig. 2). The number of BCNH observed during evening censuses declined dramatically between May 12 and May 26; counts were discontinued after that time. This decline in BCNH leaving Indian Ridge Marsh during evening hours was undoubtedly due to the increasing numbers of herons remaining at nests to incubate eggs or brood young. Also, counting became more difficult as foraging trips became shorter in duration as BCNH returned to the colony to feed young or allow their mates to recess. No BCNH were observed at Heron Pond on March 24 or 30; however, 33 BCNH were counted there on April 6. Population censuses conducted on evenings of April 29 and May 10 indicated that a substantial number of BCNH were nesting there (142 counted on May 10).

BCNH were first noted at LCW on March 22 of 2003; with the exception of a leveling off of numbers between the weeks of March 30 and April 11, numbers gradually increased from the start of the evening population censuses on March 23 through May 10, when they peaked at 641 herons (Fig. 2). The number of BCNH observed during evening censuses declined dramatically between May 10 and June 1; evening censuses were discontinued after that time. As in 2002, this decline in BCNH observed was undoubtedly due to increasing numbers of uncounted incubating/brooding herons coupled with shorter, more frequent foraging trips by observed herons. Thus, the 2003 peak count of 641 BCNH was down 15% from the 2002 peak count of 750, but the estimated number of nests ( $641 \text{ total BCNH} / 2 \text{ BCNH/nest} = 320 \text{ nests}$ ) was within “normal” limits for the period 1997–2002 (303 to 404 nests).

The peak BCNH population at LCW varied considerably during 1992–97, from a high of nearly 1,600 in 1992 to less than 600 in 2000 (Fig. 3). The quadratic trend was significant and described a relatively large proportion of the variation in peak numbers. Although there was a declining population trend during much of the 1990s, numbers have more or less stabilized at 600–800 herons in recent years.

The number of nests varied considerably during 1984–97, from a low of 266 in 1984 to a high of 871 in 1992 (Fig. 4). The cubic trend was significant and described a relatively large portion of the variation in number of nests. The number of BCNH nests increased dramati-

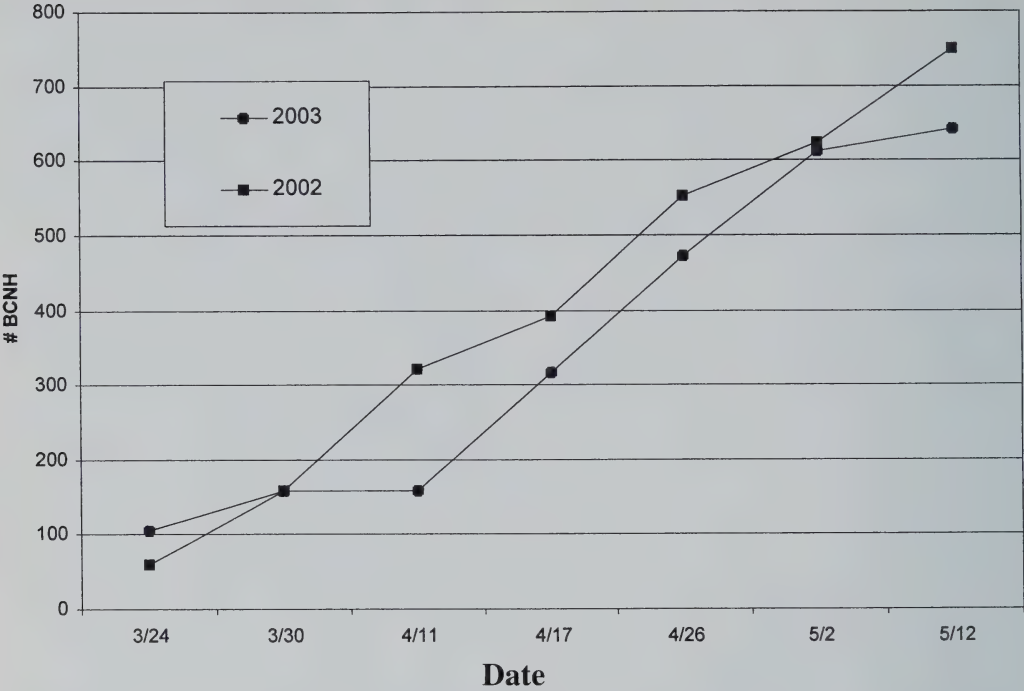


Figure 2. Results of counts of Black-crowned Night-Herons leaving nesting locations to forage during 2002 and 2003.

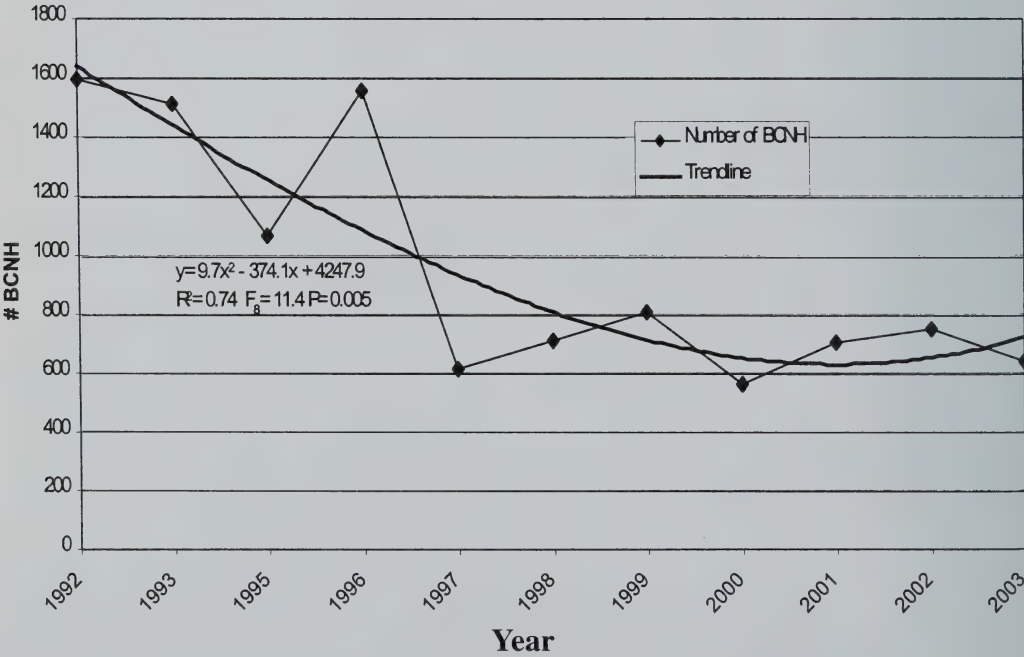


Figure 3. Peak numbers of Black-crowned Night-Herons at Lake Calumet wetlands, 1992–2003.

cally during the latter half of the 1980s and remained relatively high into the mid-1990s. Numbers of BCNH nests at LCW declined throughout much of the 1990s before essentially leveling off at 300–400 nests during the late 1990s and early 2000s (Fig. 4).

DISCUSSION

Many factors have been suggested as causes for recent declines in BCNH populations, including vandalism, disturbance at breeding colonies, drainage of wetlands, and land development for homes and recreation (Davis 1993). A relationship has been demonstrated between chlorinated hydrocarbon pesticide pollution and egg-shell thinning in herons (Faber et al. 1972). Pre-1947 (pre-DDT) and post-1947 (DDT-era) BCNH eggshell thickness measurements taken in 15 U.S. states demonstrate significantly thinner eggshells in post-1947 clutches (Ohlendorf and Marois 1990, Ohlendorf et al. 1978, Ohlendorf et al. 1977), but convincing documentation that DDT (DDE) and other pesticides have caused local BCNH population declines before DDT was banned in 1972 is lacking (Davis 1993).

High-water levels, resulting in flooded nests, have forced BCNH to relocate within LCW on numerous occasions over the past two decades. In virtually all of these cases, the BCNH completed a successful breeding season. In the Illinois River Valley of central Illinois, flooding has had an impact on heron colonies in recent years, with high water appearing to disadvantage BCNH in particular (Bjorklund and Holm 1997). The frequent and rapid flood peaks along the Illinois River have occurred as a result of floodplain constriction by levees, channelization of tributary streams, and other human activities (Bjorklund and Holm 1997).

Bjorklund and Holm (1997) found that prolonged elevated water levels at Illinois River sites during the period of nestling development (June through August) had a negative impact on the size of heron nesting populations during the following year's breeding season. Periods of major flooding along the Illinois River occurred during 1993–96, with corresponding decreases in nesting BCNH populations during that period (Bjorklund and Holm 1997). A spike in BCNH peak numbers/nests at LCW during the early

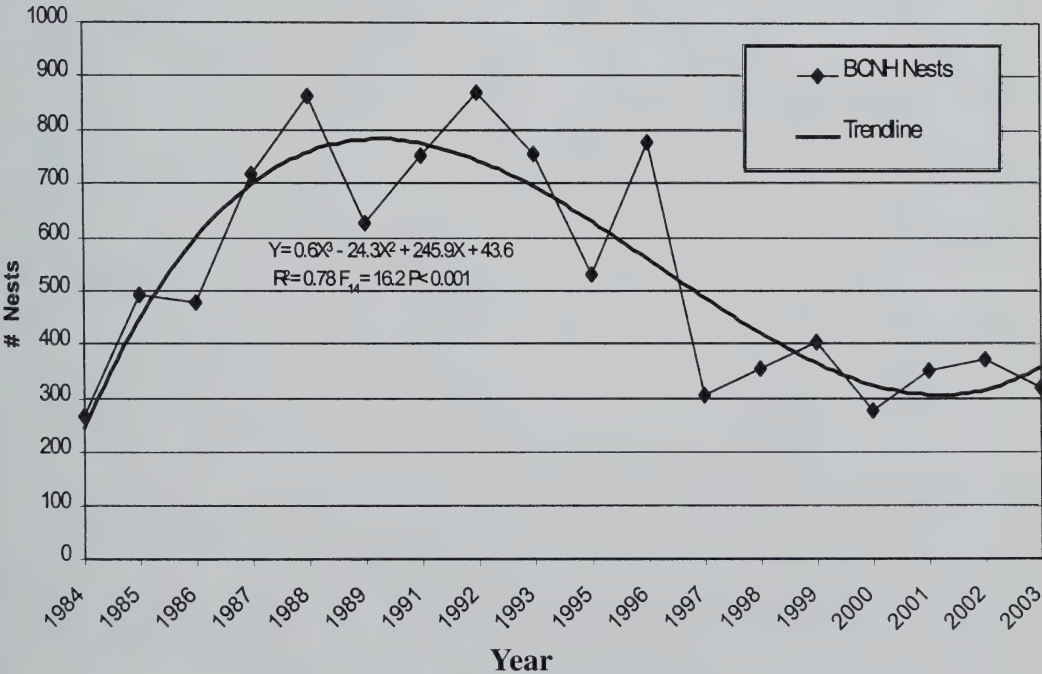


Figure 4. Number of Black-crowned Night-Heron nests at Lake Calumet wetlands, 1985–2003.



1990s corresponded to the severe flooding of the Illinois River floodplain (and resultant desertion of colonies by BCNH) during the same period, suggesting that emigration of BCNH from Illinois River colonies to LCW may have occurred during that time. The Breeding Bird Survey Trend Map (1966–1996) for BCNH also shows decreases ( $< -1.5\%$ ) in Illinois River BCNH populations, and corresponding increases ( $> +1.5\%$ ) in LCW BCNH populations during that period.

Interspecific competition for nest sites may have affected BCNH populations at various Illinois colonies. At Lake Renwick (Plainfield, Will Co., IL) Double-crested Cormorants (*Phalacrocorax auritus*) appear to have displaced Great Blue Herons (*Ardea herodias*), Great Egrets (*Ardea alba*), and BCNH from their traditional nest sites. As Double-crested Cormorant numbers increased, the BCNH population at Lake Renwick declined from 273 nests in 1983 to 57 nests in 1990 (Milosevich 1990). Numbers of Double-crested Cormorants have also increased at the Baker's Lake colony in northwestern Cook Co., while the BCNH population there declined from 220 nests in 1989 to 11 nests in 1992. It is plausible that BCNH emigrating from Lake Renwick, Baker's Lake, and other declining Illinois BCNH colonies contributed to the BCNH population increases at LCW during the late 1980s to early 1990s. The decline in the breeding population during the 1990s and relatively stable number of breeding pairs since that time suggests that LCW were ultimately unable to support a higher breeding population resulting from the emigration of BCNH from Illinois River and other colonies.

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NOTES





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# Review of the New World Genera of the Leafhopper Tribe Erythroneurini (Hemiptera: Cicadellidae: Typhlocybinae)

Christopher H. Dietrich and Dmitry A. Dmitriev

Illinois Natural History Survey Bulletin  
Volume 37, Article 5  
July 2006

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## ABSTRACT

The genus-level classification of New World Erythroneurini is revised based on results of a phylogenetic analysis of 100 morphological characters. The 704 known species are placed into 18 genera. *Erasmoneura* Young and *Eratoneura* Young, previously treated as subgenera of *Erythroneura* Fitch, and *Erythridula* Young, most recently treated as a subgenus of *Arboridia* Zachvatkin, are elevated to generic status. Three species previously included in *Erasmoneura* are placed in a new genus, *Rossmoneura* (type species, *Erythroneura tecta* McAtee). The concept of *Erythroneura* is thereby narrowed to include only those species previously included in the nominotypical subgenus. New World species previously included in *Zygina* Fieber are not closely related to the European type species of that genus and are therefore placed in new genera. *Neozygina*, n. gen., based on type species *Erythroneura ceonothana* Beamer, includes all species previously included in the “*ceonothana* group”, and *Zyginama*, n. gen., based on type species *Erythroneura ritana* Beamer, includes most species previously included in the “*ritana* group” of New World *Zygina*. Five additional new genera are described to include other previously described North American Erythroneurini: *Hepzygina*, n. gen., based on type species *Erythroneura milleri* Beamer and also including *E. aprica* McAtee; *Mexigina*, n. gen., based on type species *Erythroneura oculata* McAtee; *Nelionidia*, n. gen., based on type species *N. pueblensis*, n. sp., three additional new species, and *Erythroneura amicis* Ross; *Neoimbecilla*, n. gen., based on type species *Erythroneura kiperi* Beamer and one new species; and *Illinigina*, n. gen., based on type species *Erythroneura illinoisensis* Gillette. Five new genera, based on previously undescribed species, are also recognized: *Aztegina*, n. gen., based on *A. punctinota*, n. sp., from Mexico; *Amazygina*, n. gen., based on type species *A. decaspina*, n. sp., and three additional new species from Ecuador; *Hamagina*, n. gen., based on type species *H. spinigera*, n. sp., and two additional new species from Peru and Ecuador; *Napogina*, n. gen., based on type species *N. recta*, n. sp., and one additional new species from Ecuador; *Perugina*, n. gen., based on type species *P. denticula*, n. sp., from Peru; and *Spinigina*, n. gen., based on type species *S. hirsuta*, n. sp., and an additional new species from Peru. Phylogenetic analysis suggests that the New World Erythroneurini consist of three lineages resulting from separate invasions from the Old World.

## KEYWORDS

Homoptera, identification, leafhopper, morphology, phylogeny, taxonomy



## INTRODUCTION

The leafhopper subfamily Typhlocybinae is a diverse group of mostly tiny, delicate leafhoppers that feed preferentially on the contents of leaf parenchyma cells of their host plants. Species of this subfamily differ from other leafhoppers in lacking closed preapical cells in the forewing and in having the first hind tarsomere acuminate apically. In agroecosystems, feeding by large populations of typhlocybines causes the familiar “stippling” injury to numerous crops including soybean, potato, apple, and grape. Some species cause a more severe kind of injury known as “hopperburn” (Backus et al. 2005). Currently, Typhlocybinae comprises ca. 5,000 described species worldwide, making it the second largest leafhopper subfamily, after Deltocephalinae. Nevertheless, the diverse tropical faunas of Typhlocybinae, particularly in the New World, remain poorly documented, and it is likely that the group will eventually be found to eclipse all other leafhopper subfamilies in species richness.

The largest tribe of Typhlocybinae appears to be Erythroneurini, with 164 genera and nearly 2,000 described species. Diverse regional faunas of this tribe have been documented in the Old World tropics, particularly on the Indian subcontinent and in southeast Asia (Oman et al. 1990). Tropical parts of Africa, Madagascar, Australia, and New Guinea also appear to harbor diverse erythroneurine faunas, but these remain largely undescribed.

The previously documented New World fauna of erythroneurine leafhoppers comprises over 700 described species, all from North America. Available host plant records indicate that the vast majority of North American species feed and oviposit on woody angiosperms. Most species appear to specialize on a particular host genus or species for oviposition and nymphal development, although adults often utilize other food plants during spring and fall (Ross and DeLong 1953). Species are particularly diverse and abundant in eastern deciduous forests, from which the majority of species have been described, and where as many as 100 species have been collected from a single tree (Hepner 1976). Detailed information on the life history and ecology of the Erythroneurini of eastern North America was provided by Ross and DeLong (1953). Little is known about the ecology of the many species that occur in the

southwestern U.S., Mexico, and the Neotropics.

Prior to 1952, with the exception of seven species of *Hymetta* McAtee, all New World species of Erythroneurini were placed in the genus *Erythroneura* Fitch. In his revision of the North American fauna, Beamer (1930, 1931a, b, c, d, 1932a, c, d, e, f, g, h, 1938, 1946) recognized four species groups within *Erythroneura* based primarily on the venation and markings of the forewing: the *comes* group, the *maculata* group, the *vulnerata* group, and the *obliqua* group. Young (1952) identified additional features in the male genitalia supporting these groups and formally recognized them as subgenera by naming them, respectively, *Erythroneura* (sensu stricto), *Eratoneura* Young, *Erasmoneura* Young, and *Erythridula* Young. Young (1952) excluded some predominantly southwestern U.S. species from *Erythroneura* because the male style of these species lacks a second apical extension. These he assigned to *Zygina* Fieber, while noting that the genus as then defined constituted a “complex of considerable size and wide distribution ...doubtless destined to undergo considerable subdivision.”

Beginning in the 1970s, Dworakowska (1970a and numerous subsequent papers) embarked on a long-term project to revise the Old World fauna of Erythroneurini, reassigning nearly all Old World species previously placed in *Erythroneura* and *Zygina* to other genera and describing over 500 new species, largely from the Afrotropical and Oriental regions. To date, Dworakowska and others have described more than 150 genera and subgenera to comprise the approximately 1,200 described Old World species of Erythroneurini.

Progress on the classification of New World Erythroneurini has lagged behind that of the Old World fauna. While nearly 300 North American species have been described in the past 50 years, mostly by Hepner (1966 and subsequent papers), endemic New World species of erythroneurine leafhoppers have continued to be placed into only four genera: *Arboridia* Zachvatkin (subgenus *Erythridula*), *Erythroneura*, *Hymetta* McAtee, and *Zygina* Fieber (Young 1952, Dworakowska 1970b). Moreover, although Young (1952: 75) examined specimens of an undescribed species of the “*ceonothana* group” of *Zygina* from Argentina, not a single species of Erythroneurini, the most speciose group of typhlocybine leafhoppers in the Old World tropics, has been described from

South America. This paper is a first attempt to elucidate the phylogenetic status and relationships of New World Erythroneurini and to align the generic concepts of this fauna more closely with those currently applied to the Old World fauna.

## MATERIALS AND METHODS

To examine the phylogenetic relationships within Erythroneurini and determine the status of the New World genera, a matrix of 100 adult morphological characters was compiled for 75 exemplar Erythroneurini species and 10 outgroups. The taxon sample comprised two or more representatives of each of the previously recognized and newly described New World genera and subgenera, including the type species when possible. It was not practical to include representatives of all the recognized genera of Erythroneurini in the analysis, so exemplars of Old World genera were selected to represent a broad spectrum of the morphological diversity of the tribe. Exemplars of the typhlocybina tribes Alebrini, Dikraneurini, Empoascini, Jorumini, and Typhlocybini were included as outgroups. Phylogenetic analyses of this matrix were performed using PAUP\* 4.0 (Swofford 1998) with TBR branch swapping on 100 random taxon addition sequence replicates. Multistate characters were treated as non-additive (unordered) and trees were rooted to the outgroup taxon *Paralebra* sp. (Alebrini). Branch support was measured by calculating the decay index (Bremer 1994) for each consistently resolved node on the most parsimonious trees. This was accomplished using the "enforce topological constraints" option to search for the shortest tree(s) not compatible with each node, using the heuristic search algorithm in PAUP\*. Characters and states are listed in Appendix A. A list of species examined is given in Appendix B. The data matrix is given in Appendix C.

Morphological terminology follows Young (1952) with the following exceptions. Wing venation follows Shcherbakov (1981, 1982), with some abbreviation to reflect the reduced venation of typhlocybina leafhoppers; veins and cells are named as shown in Figs. 1-B and C. Leg chaetotaxy follows Rakitov (1998), with rows of setae designated according to their position when the leg is extended laterad (i.e., AV = anteroventral; AM = anteromedial; PD = posterodorsal, etc.). For simplicity, the angulate

projections, or points, of the male style (paramere) apex are numbered 1–3 as shown in Fig. 1-H. As in most leafhopper taxa, identification of erythroneurine species, and in many cases genera, requires clearing and examination of the male genital capsule and genitalia. Thus, keys and descriptions are based on males. At present, females of most species may only be identified through their association with males.

Specimens of newly described taxa are deposited in the insect collections of the Illinois Natural History Survey, Champaign (INHS), the U.S. National Museum of Natural History, Washington (USNM), and the Universidad Nacional Mayor de San Marcos, Lima, Peru (USML). Other specimens, including primary types of previously described species, were examined from the California Academy of Sciences, San Francisco; Canadian National Collection, Ottawa; Colorado State University, Ft. Collins; Mississippi State University, State College; North Carolina State University, Raleigh; Ohio State University, Columbus; University of Kansas, Lawrence; INHS; and USNM.

Interpretations and synonymies of previously described species follow Young (1952) and the more recent literature, unless otherwise noted. In the lists of species included in each genus, only species presently considered valid, and new synonyms, are listed. More complete synonymies will be included in subsequent treatments of the individual genera (in preparation).

## RESULTS

The phylogenetic analysis of morphological data recovered 24 equally parsimonious trees of length 1056, rescaled consistency index 0.100, and retention index 0.571. The strict consensus (Fig. 12) of these trees is well resolved with only three unresolved trichotomies. The analysis recovered Erythroneurini as monophyletic with sister group Dikraneurini. Most erythroneurine taxa were grouped into two large clades subtended by a paraphyletic grade of tropical Australasian taxa. The newly described South American genera *Spinigina*, *Napogina*, *Hamagina*, *Perugina*, and *Amazygina* together formed a monophyletic group that was sister to a clade comprising primarily Afrotropical genera. The North American genera (including *Neozygina* and



*Zyginama*, which are also represented in South America) grouped together in a large clade that also included some East Asian taxa (*Ziczacella*, *Arboridia* spp., and *Asianidia*).

The analysis supported the monophyly of the North American genera *Hymetta*, *Erythroneura* (sensu stricto), *Erasmoneura*, *Hepzygina*, n. gen., *Neozygina*, n. gen., *Zyginama*, n. gen., and *Nelionidia*, n. gen. *Eratoneura* was paraphyletic with respect to *Erythroneura*, and constraining *Eratoneura* to be monophyletic required five additional steps. *Erythridula* and *Neoimbecilla* were also paraphyletic on the most parsimonious trees. Yet, constraining these genera as monophyletic added only a single step to the length of the tree. The analysis also suggested that *Arboridia* (sensu lato) as currently defined is polyphyletic. The New World species previously placed in *Zygina* did not group with the included Old World representative of the genus. Most of the former grouped together into a clade comprising the newly described genera *Neozygina* (corresponding to the informal “*ceonothana* group” recognized by Young), *Zyginama* (comprising most species previously included in the “*ritana* species group”), *Mexigina* and *Hepzygina* (comprising additional “*ritana* group” species). Two additional species of the “*ritana* group,” were placed in a clade with *Hymetta*, and these are here included in two new genera—*Illinigina* and *Neoimbecilla*.

The analysis largely supports Ross’ (1965) hypothesis that the New World fauna of Erythroneurini originated through multiple invasions from the Old World. On the resulting cladograms, alternative equally parsimonious optimizations of the binary character

“geographic distribution,” with states (0) Old World and (1) New World, are possible. Under the parsimony criterion, the results require at least three, and are consistent with as many as four, independent origins of the various New World erythroneurine lineages (Fig. 12). A clade comprising the endemic South American genera was sister to a clade comprising mostly Afrotropical genera. The North American genera grouped into two clades, each of which had an Asian Palaearctic taxon as its sister. Nevertheless, because many of the nodes involved received low branch support, these scenarios remain questionable. Constraining the New World Erythroneurini to be monophyletic requires a minimum of nine additional steps and constraining the North American Erythroneurini to be monophyletic requires at least seven additional steps.

## TAXONOMY

### Tribe Erythroneurini Young, 1952

This tribe is a well-supported monophyletic group, characterized by the venation of the hindwing, in which the anal vein is completely confluent with the postcubital vein (Fig. 1-C: v), the submarginal vein is absent between RM and CuA, and the forewing inner (fourth) apical cell is elongate and parallel-sided. Other morphological features that appear to distinguish most members of Erythroneurini from other Typhlocybinae include the relatively broad maxillary plate, which is visible laterad of lorum throughout its length (Fig. 1-A); and the absence of an enlarged AM1 seta near the apex of the front femur (Fig. 1-D).

## Key to Adult Males of the New World Genera of Erythroneurini

- 1 Pygofer with dorsal appendage absent (small teeth may be present) (Figs. 4-I, 5-L).....2
- 1’ Pygofer with dorsal appendage well developed (may be small), rigidly attached (Fig. 1-I) or articulated to dorsal margin (Fig. 4-A) .....3
- 2 Pygofer with well developed ventral appendage, dorsal margin without teeth (Fig. 4-I); head with pair of black spots just dorsad of antennal pits in addition to paired spots on crown (south-western US and Mexico) .....*Mexigina*, n. gen.
- 2’ Pygofer without ventral appendage, dorsal margin with small teeth distally (Fig. 5-L); head without pair of black spots just dorsad of antennal pits (South America) .....*Perugina*, n. gen.



3	Pygofer with ventral appendage well developed (Fig. 1-I) (rarely, appendage absent and posteroventral margin with strongly sclerotized ridge), dorsal appendage immovably fused to dorsal margin; first segment of anal tube without spinose posterolateral lobe .....	4
3'	Pygofer without ventral appendage (or sclerotized ridge), or if small appendage present, first segment of anal tube with spinose posterolateral lobe (Fig. 5-M); dorsal pygofer appendage articulated or fused .....	7
4	Anteclypeus (Fig. 1-A) not swollen, extended to lateral margin of face only near apex; subgenital plate with angulate basolateral projection (Fig. 6-A); connective without median anterior lobe (Fig. 1-I) .....	5
4'	Anteclypeus strongly swollen and very broad, extended to lateral margin of face a considerable distance from apex; subgenital plate without angulate basolateral projection; connective with distinct median anterior lobe .....	<i>Alnetoidia alneti</i> (Dahlbom) (Palearctic species, established in Nova Scotia (Hamilton 1985))
5	Pygofer with 1–2 macrosetae just basad of dorsal appendage, ventrolateral setae inconspicuous or absent (Fig. 5-B); crown weakly produced, anterior and posterior margins parallel, with pair of well delimited brown or black preapical spots (Fig. 2-M) .....	<i>Neozygina</i> , n. gen.
5'	Pygofer without macrosetae just basad of dorsal appendage, ventrolateral setae usually large, conspicuous (Fig. 1-E); crown with anterior margin usually more produced than posterior margin, with or without paired preapical spots (Fig. 2-O) .....	6
6	Aedeagus with large unpaired dorsal process between phallobase and gonopore-bearing shaft (Fig. 9-A); subgenital plate with or without large dorsoapical spine (Fig. 5-H)....	<i>Hamagina</i> , n. gen.
6'	Aedeagus without large unpaired dorsal process between phallobase and gonopore-bearing shaft; subgenital plate without dorsoapical spine (Fig. 1-I) .....	<i>Zyginama</i> , n. gen.
7	Style apex attenuate or broad and truncate, often footlike, apex with no more than two points (Fig. 1-I) .....	8
7'	Style apex with three points (third point sometimes reduced to obtusangular projection) (Fig. 1-H) .....	15
8	Pygofer lobe and dorsal membrane conspicuously clothed with long fine setae; connective with well-developed median anterior lobe; subgenital plate without basolateral row of three or more macrosetae .....	<i>Zygina flammigera</i> (Fourcroy) (Palearctic species, established in coastal western North America (Hamilton 1983))
8'	Pygofer lobe and dorsal membrane without conspicuous long fine setae; connective (Fig. 1-I) without median anterior lobe; subgenital plate with basolateral row of three or more macrosetae (Fig. 1-E) (Nearctic and Neotropical) .....	9
9	Pygofer with dorsal appendage fused to margin, without basal articulation or line of weakening (Fig. 1-E); dorsal apodeme of aedeagus without sclerotized connection to pygofer.....	10
9'	Pygofer with dorsal appendage either freely articulated or with distinct basal line of weakening separating it from pygofer margin (Fig. 4-A); dorsal apodeme of aedeagus connected to pygofer by pair of sclerotized arms (Figs. 6-I, J) .....	14
10	Aedeagus with paired processes, when present, arising near base (Fig. 8E, F); with or without large unpaired process arising either anterodorsad or posteroventrad of gonopore-bearing shaft ...	11
10'	Aedeagus with paired distal processes present (Fig. 1-G), without large unpaired process other than gonopore-bearing shaft .....	12

- 11 Unpaired aedeagal process, when present, arising anterodorsad of gonopore-bearing shaft (Figs. 8-I, M); scutellum apex pale; crown unmarked or with unpaired medial macula (South America) .....*Amazygina*, n. gen.
- 11' Unpaired aedeagal process arising posteroventrad of gonopore-bearing shaft (Fig. 6-F); scutellum apex black; crown with or without paired spots (Mexico and USA) .....*Hepzygina*, n. gen.
- 12 Pygofer with basolateral setae fine, inconspicuous (Fig. 4-F); style apex short, footlike, with imbricate texture (Fig. 6-E) (Mexico) .....*Aztegina*, n. gen.
- 12' Pygofer with basolateral setae enlarged, conspicuous (Fig. 5-J); style apex usually not footlike (Fig. 10-C), but if so, then glabrous (Fig. 10H) (South America) .....13
- 13 First segment of anal tube with pair of spinose posterolateral lobes; pygofer with appendage arcuate (Figs. 5-M, N) .....*Spinigina*, n. gen.
- 13' First segment of anal tube without pair of spinose posterolateral lobes; pygofer with appendage not elevated above margin of distal lobe (Figs. 5-J, K) .....*Napogina*, n. gen.
- 14 Forewing (Figs. 2-E, 3-E) broad, marked with numerous small red or brown flecks, scutellum elevated and shelflike posteriorly .....*Hymetta* McAtee
- 14' Forewing (Figs. 2-H, 3-H) narrow, with few larger brown or red spots, scutellum not elevated posteriorly .....*Illinigina*, n. gen.
- 15 Pygofer appendage rigidly attached to pygofer, without basal suture (Fig. 4-C); crown without pair of brown spots preapically; forewing vein CuA usually shorter than CuP, base of inner apical cell usually with small dark spot (Fig. 3-B) .....16
- 15' Pygofer appendage movably articulated to pygofer (Fig. 4-A) or at least with basal line of weakening (or, if pygofer appendage rigidly attached, then crown with pair of brown spots preapically); forewing vein CuA approximately same length as CuP, base of inner apical cell usually without small dark spot (Figs. 3-D, G) .....17
- 16 Forewing with base of inner apical cell transverse (Fig. 1-B), CuA very short or absent, second apical cell often with brown spot near apex; pygofer appendage C-shaped (ventral arm of C may be branched), without digitiform basal process (Fig. 4-B); aedeagal shaft usually without denticuli .....*Erythroneura* Fitch
- 16' Forewing with base of inner apical cell oblique, CuA usually longer, second apical cell without dark spot apically (Fig. 3-C); pygofer appendage a simple spinelike process (Fig. 4-C), bifid in some species, with small digitiform internal process at base; aedeagal shaft usually with denticuli .....*Eratoneura* Young
- 17 Style apex with third point greatly elongate and curved mesad, much longer than distance between first two points (Figs. 7-Q, T) .....*Neoimbecilla*, n. gen.
- 17' Style apex with third point short and straight, usually little if any longer than distance between first two points (Fig. 1-H) .....18
- 18 Pygofer with basolateral setae undifferentiated, inconspicuous; dorsal coloration usually predominantly pale yellow or white with bold longitudinal orange or red lines; crown without pair of brown preapical spots (Fig. 2-A) .....*Erythridula* Young
- 18' Pygofer basolateral setae well differentiated, conspicuous (Fig. 4-D); dorsal coloration various, usually dark orange or brown with paler markings, never consisting of bold longitudinal lines; crown with or without pair of brown preapical spots (Figs. 2-D, J) .....19
- 19 Aedeagal shaft elongate, slender, with pair of long recurved lateral processes apically and median anterior preapical lobe or spine, preatrium much shorter than shaft (Fig. 7-A); crown pale with pair of dark preapical spots (Fig. 2-J) .....*Nelionidia*, n. gen.
- 19' Aedeagal shaft short, paired processes short or absent, preatrium longer than shaft; crown with or without dark preapical spots .....20

- 20 Aedeagal shaft (Figs. 7-Y, Z) without paired spines or processes, with unpaired posterior preapical spine; crown only slightly longer medially than next to eye, usually with pair of dark preapical spots (Fig. 2-N) .....*Rossmoneura*, n. gen.
- 20' Aedeagal shaft with paired spines or processes, without unpaired posterior preapical spine; crown distinctly longer medially than next to eye, usually mostly dark brown (Fig. 2-D), but if pale, then without pair of dark preapical spots .....*Erasmoneura* Young

Status of Previously Described Taxa

Old World Genera that Previously Included  
New World Species

*Arboridia* Zachvatkin

*Arboridia* Zachvatkin 1946:153 (type species  
*Typhlocyba parvula* Boheman)  
*Khoduma* Dworakowska 1972b:153 (type spe  
cies: *K. jacobii* Dworakowska)

**Notes.** *Arboridia* was originally described by Zachvatkin (1946), as a subgenus of *Zyginidia* Haupt, to accommodate a number of western Palaearctic species, including those placed by Ribaut (1936) in his “*Erythroneura parvula* group.” Dworakowska (1970b) elevated *Arboridia* to generic rank and transferred the subgenus *Erythridula* Young (erected by Young, 1952, as a subgenus of *Erythroneura*) to *Arboridia*, continuing to treat the former as a subgenus. She noted that *Erythridula* differs from *Arboridia* (sensu stricto) in having the head more strongly produced, the face wider ventrally, the second apical cell of the forewing narrower and the fourth wider. She also noted that *Erythridula* and *Arboridia* differ dramatically in coloration. Most *Erythridula* species have the dorsum pale overall with bold longitudinal red or orange stripes on the head and thorax (including forewing); they also lack paired black spots on the vertex. In contrast, Palaearctic species of *Arboridia* (s.s.) lack bold longitudinal stripes, the crown has a pair of black preapical spots, the mesonotum has black basolateral triangles, and the body including the abdomen is heavily marked with dark brown or black. Although the structure of the male genital capsule and genitalia of *Arboridia* (s.s.) and *Erythridula* are very similar, species of the latter have the macrosetae of the subgenital plate considerably larger and male sternite IX usually has a median longitudinal internal ridge anteriorly that is usually absent in *Arboridia* (s.s.).

European species of *Arboridia* also have the male subgenital plates broader overall with the lateral margin rounded basally, and the ventral angle of the style apex is situated distad of the dorsal fold of the subgenital plate. *Erythridula* have the plates much narrower with the lateral margin distinctly angulate basally, and the ventral angle of the style apex is even with or basad of the dorsal fold of the subgenital plate. These features, in combination with other differences noted by Dworakowska, as well as the non-overlapping geographic distributions of the two groups, seem sufficient to justify elevating *Erythridula* to generic rank (see below), thus restricting *Arboridia* to include only the nominotypical subgenus and subgenus *Arborifera* Sohi and Sandhu (misspelled as “*Arboridula*” by Dworakowska and Viraktamath 1975 and Dworakowska 1980).

Species from the Oriental region currently placed in *Arboridia* (Dworakowska and Viraktamath 1975; Dworakowska 1979, 1980; Sohi and Dworakowska 1984), although sharing similar pygofer structure and chaetotaxy with both the Palaearctic *Arboridia* and the Nearctic *Erythridula*, differ considerably in other respects. These species mostly lack well-developed paired spots on the crown and longitudinal stripes on the dorsum, and many lack a third point at the style apex.

The morphology-based phylogenetic analysis, which included five species of *Erythridula* and seven representatives of Old World *Arboridia*, grouped *Erythridula* in a paraphyletic grade (one step shorter than a tree constrained to include a monophyletic *Erythridula*) but indicated that the Old World *Arboridia* may be polyphyletic (Fig. 12). Thus, although some Oriental species of *Arboridia* have already been placed in a separate subgenus (*Arborifera*), one or more additional genera or subgenera may eventually need to be erected to receive various “*Arboridia*” species from the Oriental region and the Middle East.



Under the concept of the genus adopted here, *Arboridia* is restricted to the Old World.

### *Zygina* Fieber

*Zygina* Fieber 1866a:509 (type species: *Typhlocyba nivea* Mulsant and Rey)

*Flammigeroidia* Dlabola 1958c:56 (type species: "*Erythroneura flammigera* Geoffr" = *Cicada flammigera* Fourcroy)

**Notes.** In his classification of Western Hemisphere Typhlocybinae, Young (1952) redefined *Zygina*, which previously had been treated as a synonym of *Erythroneura* by Ribaut (1936), to include "all those leafhoppers with a single broad extension of the style apex." Based on their lack of a third point ("second extension" in Young's terminology) of the male style, Young placed in *Zygina* all New World erythroneurines that had been included by previous authors in the informal "Western Obliqua group" of *Erythroneura* (DeLong and Knull 1946).

Although Young's revision treated only the New World fauna, he noted that Oriental species included in *Zygina* by Matsumura (1931) appeared to have been placed accurately and that many additional Old World erythroneurine species were referable to the "*Zygina* complex." Some subsequent authors followed Young's broad definition of the genus and placed various New Zealand, African, and Oriental species in *Zygina*.

More recently, the definition of *Zygina* has been narrowed considerably and Dworakowska (1970c) included only Palaearctic species. Under this definition, the genus includes species having the following combination of features: male pygofer with conspicuous setae laterally and on dorsal membrane, dorsal appendage small, slender, and not movably articulated; subgenital plate with basolateral projection absent and macrosetae distributed mostly beyond midlength; style apex with two points, preapical lobe weakly developed.

Excluded from this definition are all New World species included in *Zygina* by Young (1952). Phylogenetic analysis indicated that these species are not closely related to the Palaearctic species of the genus. Based on this analysis, the species are here included in seven new genera, described below.

One Palaearctic species, *Zygina flammigera* (Fourcroy), has become established in the New

World and is recorded from Washington state and British Columbia (Hamilton 1983).

### New World Genera

#### *Erythridula* Young, 1952, new status

*Erythroneura* (*Erythridula*) Young 1952:81  
(type species: *Tettigonia obliqua* Say)  
*Arboridia* (*Erythridula*) Dworakowska  
1970b:615

**Diagnosis.** This genus differs from other New World Erythroneurini in having the following combination of features: ground color usually pale, often with bold longitudinal red or orange stripes (Fig. 2-A); crown without pair of brown or black spots; forewing apical cells without dark spots, inner apical cell with base oblique (Fig. 3-A); male pygofer without ventral appendage or sclerotized ridge, dorsal appendage freely articulated, basolateral setae fine and inconspicuous (Fig. 4-A); style apex with three angulate projections.

**Distribution.** Temperate North America.

**Notes.** The phylogenetic analysis recovered *Erythridula* as paraphyletic, but constraining the included species to form a monophyletic group added only one step to the tree. Despite the lack of support for a monophyletic *Erythridula*, species in this genus are readily distinguishable from other North American Erythroneurini by the features given in the key. Thus, *Erythridula* is treated as a distinct taxon, pending more detailed analyses. As noted above, despite similarities in the structure of the male genital capsule, consistent differences in external morphology suffice to justify treating *Erythridula* as a distinct genus, rather than as a subgenus of *Arboridia*. *Erythridula* presently comprises 256 species, all of which are apparently restricted to North America. A specimen-level database and interactive key to species are available on-line at [http://ctap.inhs.uiuc.edu/dmitriev/3i\\_keys.asp](http://ctap.inhs.uiuc.edu/dmitriev/3i_keys.asp).

**Included species:**

*Erythridula abolla* (McAtee, 1920a:285) (*Erythroneura*), new combination  
*Erythridula accurata* (Beamer, 1934b:18 n.nov.) (*Erythroneura*), new combination  
*Erythridula acicularis* (Beamer, 1932i:126) (*Erythroneura*), new combination  
*Erythridula acutalis* (Ross & DeLong, 1953a:83) (*Erythroneura*), new combination  
*Erythridula adae* (Hepner, 1977c:363) (*Erythroneura*), new combination  
*Erythridula ador* (McAtee, 1918b:361) (*Erythroneura*), new combination  
*Erythridula aenea* (Beamer, 1930b:436) (*Erythroneura*), new combination  
*Erythridula aesculella* (Ross & DeLong, 1953a:82) (*Erythroneura*), new combination  
*Erythridula afflicta* (Beamer, 1935a:101) (*Erythroneura*), new combination  
*Erythridula alata* (Knull, 1946a:45) (*Erythroneura*), new combination  
*Erythridula albanyensis* (Hepner, 1976b:124) (*Erythroneura*), new combination  
*Erythridula albescens* (Beamer, 1930b:443) (*Erythroneura*), new combination  
*Erythridula amabilis* (McAtee, 1924d:132) (*Erythroneura*), new combination  
*Erythridula ampaiae* (Hepner, 1976d:314) (*Erythroneura*), new combination  
*Erythridula ampasa* (Ross & DeLong, 1953a:86) (*Erythroneura*), new combination  
*Erythridula ampla* (Knull, 1951c:179) (*Erythroneura*), new combination  
*Erythridula andrewsi* (Hepner, 1976b:121) (*Erythroneura*), new combination  
*Erythridula angularis* (Beamer, 1930b:447) (*Erythroneura*), new combination  
*Erythridula anomala* (Knull, 1946a:46) (*Erythroneura*), new combination  
*Erythridula apta* (Beamer, 1935a:102) (*Erythroneura*), new combination  
*Erythridula aspera* (Beamer & Griffith, 1935a:18) (*Erythroneura*), new combination  
*Erythridula atrimucronata* (Beamer, 1930b:424) (*Erythroneura*), new combination  
*Erythridula autenae* (Johnson, 1935a:73) (*Erythroneura*), new combination  
*Erythridula barbarae* (Hepner, 1978a:134) (*Erythroneura*), new combination  
*Erythridula barnesae* (Hepner, 1976d:313) (*Erythroneura*), new combination  
*Erythridula beckiae* (Hepner, 1978a:131) (*Erythroneura*), new combination  
*Erythridula belindae* (Hepner, 1976a:207) (*Erythroneura*), new combination  
*Erythridula benedicti* (Hepner, 1976b:124) (*Erythroneura*), new combination  
*Erythridula betulaspera* (Richards & Varty, 1964a:515) (*Erythroneura*), new combination  
*Erythridula bicornis* (Beamer, 1930b:450) (*Erythroneura*), new combination  
*Erythridula bitincta* (McAtee, 1926c:130) (*Erythroneura*), new combination  
*Erythridula boniorum* (Hepner, 1976b:125) (*Erythroneura*), new combination  
*Erythridula bowmanorum* (Hepner, 1977c:362) (*Erythroneura*), new combination  
*Erythridula brundusa* (Robinson, 1924b:155) (*Erythroneura*), new combination  
*Erythridula brundusoides* (Hepner, 1976d:315) (*Erythroneura*), new combination  
*Erythridula caldwelli* (Johnson, 1935a:69) (*Erythroneura*), new combination  
*Erythridula camirei* (Hepner, 1976b:119) (*Erythroneura*), new combination  
*Erythridula carmiensis* (Hepner, 1976d:316) (*Erythroneura*), new combination  
*Erythridula caryaglabrae* (Hepner, 1977a:250) (*Erythroneura*), new combination  
*Erythridula cauta* (Beamer, 1935a:100) (*Erythroneura*), new combination  
*Erythridula cautoides* (Hepner, 1977c:363) (*Erythroneura*), new combination  
*Erythridula cavena* (Auten & Johnson, 1936a:61) (*Erythroneura*), new combination  
*Erythridula celebrata* (Johnson, 1935a:82) (*Erythroneura*), new combination  
*Erythridula chambersi* (Hepner, 1976a:208) (*Erythroneura*), new combination  
*Erythridula chandleri* (Hepner, 1976c:296) (*Erythroneura*), new combination  
*Erythridula clarysae* (Hepner, 1976c:299) (*Erythroneura*), new combination  
*Erythridula clavata* (DeLong, 1916a:105) (*Typhlocyba*), new combination  
*Erythridula clavatooides* (Hepner, 1978a:131) (*Erythroneura*), new combination  
*Erythridula cliffordi* (Hepner, 1976c:293) (*Erythroneura*), new combination  
*Erythridula cliftoni* (Hepner, 1977c:363) (*Erythroneura*), new combination  
*Erythridula clydei* (Hepner, 1977c:363) (*Erythroneura*), new combination  
*Erythridula coarctata* (Beamer, 1930b:436) (*Erythroneura*), new combination  
*Erythridula coleyi* (Hepner, 1977a:254) (*Erythroneura*), new combination



*Erythridula collinsi* (Hepner, 1977c:364) (*Erythroneura*), new combination  
*Erythridula complicata* (Johnson, 1935a:87) (*Erythroneura*), new combination  
*Erythridula contrasta* (Auten & Johnson, 1936a:62) (*Erythroneura*), new combination  
*Erythridula cooni* (Hepner, 1976b:121) (*Erythroneura*), new combination  
*Erythridula cornipes* (Beamer, 1930b:449) (*Erythroneura*), new combination  
*Erythridula cotidiana* (Beamer, 1930b:433) (*Erythroneura*), new combination  
*Erythridula cataegi* (Johnson, 1935a:61) (*Erythroneura*), new combination  
*Erythridula crevecoeuri* (Gillette, 1898a:767) (*Typhlocyba*), new combination  
*Erythridula crossi* (Hepner, 1976a:210) (*Erythroneura*), new combination  
*Erythridula cruciformis* (Beamer, 1930b:443) (*Erythroneura*), new combination  
*Erythridula cuneata* (Beamer, 1930b:433) (*Erythroneura*), new combination  
*Erythridula cuneatoides* (Hepner, 1977c:364) (*Erythroneura*), new combination  
*Erythridula curtaega* (Hepner, 1976d:313) (*Erythroneura*), new combination  
*Erythridula davichi* (Hepner, 1977a:248) (*Erythroneura*), new combination  
*Erythridula decorata* (Auten & Johnson, 1936a:63) (*Erythroneura*), new combination  
*Erythridula diana* (Hepner, 1976a:205) (*Erythroneura*), new combination  
*Erythridula diffusa* (Beamer, 1930b:434) (*Erythroneura*), new combination  
*Erythridula divisa* (McAtee, 1924c:37) (*Erythroneura*), new combination  
*Erythridula dolosa* (Beamer & Griffith, 1935a:19) (*Erythroneura*), new combination  
*Erythridula dorisae* (Hepner, 1976a:204) (*Erythroneura*), new combination  
*Erythridula dowelli* (Beamer, 1932b:62) (*Erythroneura*), new combination  
*Erythridula dunni* (Hepner, 1976c:295) (*Erythroneura*), new combination  
*Erythridula edgari* (Hepner, 1976c:300) (*Erythroneura*), new combination  
*Erythridula electa* (McAtee, 1920a:282) (*Erythroneura*), new combination  
*Erythridula eluta* (McAtee, 1920a:277) (*Erythroneura*), new combination  
*Erythridula enata* (Knull, 1951c:179) (*Erythroneura*), new combination  
*Erythridula enatoides* (Hepner, 1977c:365) (*Erythroneura*), new combination  
*Erythridula enatoidensis* (Hepner, 1976b:126) (*Erythroneura*), new combination  
*Erythridula extima* (Beamer, 1939a:29) (*Erythroneura*), new combination  
*Erythridula extimoides* (Hepner, 1976d:314) (*Erythroneura*), new combination  
*Erythridula fagiphylla* (Hepner, 1977a:254) (*Erythroneura*), new combination  
*Erythridula falcata* (Beamer, 1930b:432) (*Erythroneura*), new combination  
*Erythridula florida* (Ross & DeLong, 1953a:82) (*Erythroneura*), new combination  
*Erythridula floridoides* (Hepner, 1978a:133) (*Erythroneura*), new combination  
*Erythridula fragilis* (Johnson, 1935a:93) (*Erythroneura*), new combination  
*Erythridula frazieri* (Hepner, 1976a:210) (*Erythroneura*), new combination  
*Erythridula freta* (Knull, 1951c:179) (*Erythroneura*), new combination  
*Erythridula fretoides* (Hepner, 1977c:364) (*Erythroneura*), new combination  
*Erythridula frisoni* (Ross & DeLong, 1953a:80) (*Erythroneura*), new combination  
*Erythridula fultonae* (Hepner, 1976d:314) (*Erythroneura*), new combination  
*Erythridula fulvocephala* (Robinson, 1924b:155) (*Erythroneura*), new combination  
*Erythridula fumida* (Gillette, 1898a:758) (*Typhlocyba*), new combination  
*Erythridula funesta* (Beamer, 1930b:441) (*Erythroneura*), new combination  
*Erythridula furcillata* (Beamer, 1930b:452) (*Erythroneura*), new combination  
*Erythridula garretsoni* (Hepner, 1976c:295) (*Erythroneura*), new combination  
*Erythridula gladysae* (Hepner, 1976d:315) (*Erythroneura*), new combination  
*Erythridula gleditsia* (Beamer, 1930b:437) (*Erythroneura*), new combination  
*Erythridula hamata* (Beamer, 1930b:446) (*Erythroneura*), new combination  
*Erythridula hamiltoni* (Hepner, 1977b:52) (*Erythroneura*), new combination  
*Erythridula hamlinorum* (Hepner, 1977c:362) (*Erythroneura*), new combination  
*Erythridula harei* (Hepner, 1977a:255) (*Erythroneura*), new combination  
*Erythridula harpax* (Beamer, 1930b:432) (*Erythroneura*), new combination  
*Erythridula harrisi* (Hepner, 1976a:210) (*Erythroneura*), new combination  
*Erythridula haspata* (Ross & DeLong, 1953a:85) (*Erythroneura*), new combination



*Erythridula herberti* (Hepner, 1976d:312) (*Erythroneura*), new combination  
*Erythridula hildae* (Hepner, 1977c:362) (*Erythroneura*), new combination  
*Erythridula hormchunae* (Hepner, 1976b:120) (*Erythroneura*), new combination  
*Erythridula idonea* (Beamer, 1935a:100) (*Erythroneura*), new combination  
*Erythridula ilexae* (Hepner, 1976d:315) (*Erythroneura*), new combination  
*Erythridula ilicis* (Ross, 1953b:189) (*Erythroneura*), new combination  
*Erythridula inconspicua* (Johnson, 1935a:90) (*Erythroneura*), new combination  
*Erythridula infinita* (Beamer, 1930b:446) (*Erythroneura*), new combination  
*Erythridula insigna* (Beamer & Griffith, 1935a:17) (*Erythroneura*), new combination  
*Erythridula intricata* (Johnson, 1935a:86) (*Erythroneura*), new combination  
*Erythridula isei* (Hepner, 1977b:54) (*Erythroneura*), new combination  
*Erythridula ivae* (Hepner, 1976c:297) (*Erythroneura*), new combination  
*Erythridula ivani* (Hepner, 1976d:312) (*Erythroneura*), new combination  
*Erythridula jeanae* (Hepner, 1976a:205) (*Erythroneura*), new combination  
*Erythridula joanneae* (Hepner, 1978a:133) (*Erythroneura*), new combination  
*Erythridula jocosa* (Beamer, 1935a:101) (*Erythroneura*), new combination  
*Erythridula jonesi* (Hepner, 1976c:294) (*Erythroneura*), new combination  
*Erythridula juglandacea* (Ross & DeLong, 1953a:78) (*Erythroneura*), new combination  
*Erythridula juglandis* (Knull & Auten, 1938a:532) (*Erythroneura*), new combination  
*Erythridula juncea* (Beamer, 1937a:10) (*Erythroneura*), new combination  
*Erythridula kanensis* (Hepner, 1976d:314) (*Erythroneura*), new combination  
*Erythridula kanza* (Robinson, 1924a:58) (*Erythroneura*), new combination  
*Erythridula kennethi* (Hepner, 1976c:298) (*Erythroneura*), new combination  
*Erythridula kingstoniensis* (Hepner, 1976b:124) (*Erythroneura*), new combination  
*Erythridula lasteri* (Hepner, 1977a:248) (*Erythroneura*), new combination  
*Erythridula latapex* (Beamer, 1930b:447) (*Erythroneura*), new combination  
*Erythridula lauriphylla* (Hepner, 1978a:134) (*Erythroneura*), new combination  
*Erythridula lawsoniana* (Baker, 1926a:347 n.nov.) (*Erythroneura*), new combination  
*Erythridula leforsorum* (Hepner, 1977c:360) (*Erythroneura*), new combination  
*Erythridula lemnisca* (McAtee, 1926c:131) (*Erythroneura*), new combination  
*Erythridula leucophylla* (Hepner, 1977b:55) (*Erythroneura*), new combination  
*Erythridula lianae* (Hepner, 1976b:125) (*Erythroneura*), new combination  
*Erythridula lindleyi* (Hepner, 1976a:207) (*Erythroneura*), new combination  
*Erythridula lloydi* (Hepner, 1977a:253) (*Erythroneura*), new combination  
*Erythridula loisae* (Hepner, 1978a:138) (*Erythroneura*), new combination  
*Erythridula lucileae* (Hepner, 1976c:299) (*Erythroneura*), new combination  
*Erythridula lusoria* (Van Duzee, 1924a:234) (*Erythroneura*), new combination  
*Erythridula lyratae* (Ross & DeLong, 1953a:83) (*Erythroneura*), new combination  
*Erythridula lyratiphylla* (Hepner, 1977b:55) (*Erythroneura*), new combination  
*Erythridula magnacalx* (Beamer, 1930b:451) (*Erythroneura*), new combination  
*Erythridula malleiformis* (Beamer, 1930b:449) (*Erythroneura*), new combination  
*Erythridula mansueta* (Beamer, 1935a:98) (*Erythroneura*), new combination  
*Erythridula martini* (Hepner, 1976a:207) (*Erythroneura*), new combination  
*Erythridula maryae* (Hepner, 1976d:313) (*Erythroneura*), new combination  
*Erythridula mcomasi* (Hepner, 1978a:138) (*Erythroneura*), new combination  
*Erythridula meridiana* (Hepner, 1977b:53) (*Erythroneura*), new combination  
*Erythridula merkli* (Hepner, 1977a:253) (*Erythroneura*), new combination  
*Erythridula minima* (Johnson, 1935a:92) (*Erythroneura*), new combination  
*Erythridula minuta* (Johnson, 1935a:93) (*Erythroneura*), new combination  
*Erythridula mitlini* (Hepner, 1977a:250) (*Erythroneura*), new combination  
*Erythridula modica* (Beamer, 1930b:448) (*Erythroneura*), new combination  
*Erythridula morelandi* (Hepner, 1976d:316) (*Erythroneura*), new combination  
*Erythridula morrisi* (Hepner, 1977a:251) (*Erythroneura*), new combination  
*Erythridula nava* (Beamer, 1935a:102) (*Erythroneura*), new combination

*Erythridula navoides* (Hepner, 1977b:50) (*Erythroneura*), new combination  
*Erythridula nebekeri* (Hepner, 1976b:120) (*Erythroneura*), new combination  
*Erythridula neeli* (Hepner, 1976b:121) (*Erythroneura*), new combination  
*Erythridula newtonensis* (Hepner, 1978a:133) (*Erythroneura*), new combination  
*Erythridula nigriphylla* (Hepner, 1977b:54) (*Erythroneura*), new combination  
*Erythridula niida* (Beamer, 1935a:103) (*Erythroneura*), new combination  
*Erythridula noeva* (Gillette, 1898a:757) (*Typhlocyba*), new combination  
*Erythridula noevoides* (Ross & DeLong, 1953a:83) (*Erythroneura*), new combination  
*Erythridula nondescripta* (Johnson, 1935a:92) (*Erythroneura*), new combination  
*Erythridula normanti* (Hepner, 1976b:120) (*Erythroneura*), new combination  
*Erythridula obliqua* (Say, 1825a:342) (*Tettigonia*), new combination  
*Erythridula obvia* (Beamer, 1930b:439) (*Erythroneura*), new combination  
*Erythridula odettae* (Hepner, 1977c:362) (*Erythroneura*), new combination  
*Erythridula ohioensis* (Knull, 1945b:108) (*Erythroneura*), new combination  
*Erythridula pagodifoliae* (Hepner, 1977b:52) (*Erythroneura*), new combination  
*Erythridula paigae* (Hepner, 1976a:208) (*Erythroneura*), new combination  
*Erythridula paramera* (Hepner, 1978a:137) (*Erythroneura*), new combination  
*Erythridula parrotti* (Hepner, 1977a:251) (*Erythroneura*), new combination  
*Erythridula parsonsi* (Hepner, 1976c:295) (*Erythroneura*), new combination  
*Erythridula parvispicata* (Beamer, 1930b:435) (*Erythroneura*), new combination  
*Erythridula patricki* (Hepner, 1976a:208) (*Erythroneura*), new combination  
*Erythridula pecanae* (Hepner, 1976c:297) (*Erythroneura*), new combination  
*Erythridula penelutea* (Beamer, 1930b:427) (*Erythroneura*), new combination  
*Erythridula penenoeva* (Beamer, 1930b:438) (*Erythroneura*), new combination  
*Erythridula penetura* (Hepner, 1978a:135) (*Erythroneura*), new combination  
*Erythridula penobliqua* (Beamer, 1930b:453) (*Erythroneura*), new combination  
*Erythridula perita* (Beamer, 1935a:99) (*Erythroneura*), new combination  
*Erythridula pfrimmeri* (Hepner, 1977b:49) (*Erythroneura*), new combination  
*Erythridula phelliphylla* (Hepner, 1977b:54) (*Erythroneura*), new combination  
*Erythridula pietersi* (Hepner, 1978a:137) (*Erythroneura*), new combination  
*Erythridula plena* (Beamer, 1930b:442) (*Erythroneura*), new combination  
*Erythridula ponderosa* (Auten & Johnson, 1936a:62) (*Erythroneura*), new combination  
*Erythridula praecisa* (Knull, 1946a:46) (*Erythroneura*), new combination  
*Erythridula pura* (Knull, 1954d:38) (*Erythroneura*), new combination  
*Erythridula quadrata* (Beamer, 1930b:435) (*Erythroneura*), new combination  
*Erythridula quadratoides* (Hepner, 1977b:51) (*Erythroneura*), new combination  
*Erythridula repleta* (Johnson, 1935a:78) (*Erythroneura*), new combination  
*Erythridula rhododendronae* (Hepner, 1978a:134) (*Erythroneura*), new combination  
*Erythridula rolandi* (Hepner, 1977c:364) (*Erythroneura*), new combination  
*Erythridula rosenkranzi* (Hepner, 1977a:254) (*Erythroneura*), new combination  
*Erythridula rubens* (Beamer, 1930b:439) (*Erythroneura*), new combination  
*Erythridula rubiphylla* (Hepner, 1977b:52) (*Erythroneura*), new combination  
*Erythridula rubrataeniensis* (Beamer, 1930b:440) (*Erythroneura*), new combination  
*Erythridula rubroscuta* (Gillette, 1898a:755) (*Typhlocyba*), new combination  
*Erythridula rubrotincta* (Johnson, 1935a:91) (*Erythroneura*), new combination  
*Erythridula rufostigmosa* (Beamer, 1930b:429) (*Erythroneura*), new combination  
*Erythridula rugosae* (Ross & DeLong, 1953a:80) (*Erythroneura*), new combination  
*Erythridula sabita* (Sinha & Beamer, 1954a:105) (*Erythroneura*), new combination  
*Erythridula sagittata* (Beamer, 1930b:440) (*Erythroneura*), new combination  
*Erythridula saileri* (Hepner, 1977a:253) (*Erythroneura*), new combination  
*Erythridula salmoides* (Ross & DeLong, 1953a:83) (*Erythroneura*), new combination  
*Erythridula schusteri* (Hepner, 1976b:120) (*Erythroneura*), new combination  
*Erythridula scissa* (Beamer, 1930b:448) (*Erythroneura*), new combination  
*Erythridula scytha* (Auten & Johnson, 1936a:61) (*Erythroneura*), new combination

*Erythridula shanklandi* (Hepner, 1978a:137) (*Erythroneura*), new combination  
*Erythridula sikorowskii* (Hepner, 1976a:210) (*Erythroneura*), new combination  
*Erythridula similalis* (Ross & DeLong, 1953a:82) (*Erythroneura*), new combination  
*Erythridula sincera* (Johnson, 1935a:94) (*Erythroneura*), new combination  
*Erythridula sinua* (Johnson, 1935a:82) (*Erythroneura*), new combination  
*Erythridula solomoni* (Hepner, 1977a:251) (*Erythroneura*), new combination  
*Erythridula spatulata* (Beamer, 1930b:444) (*Erythroneura*), new combination  
*Erythridula spearca* (Johnson & Auten, 1936a:818 n.nov.) (*Erythroneura*), new combination  
*Erythridula stolata* (McAtee, 1920a:279) (*Erythroneura*), new combination  
*Erythridula stulta* (Auten & Johnson, 1936a:64) (*Erythroneura*), new combination  
*Erythridula stylata* (Johnson, 1935a:78) (*Erythroneura*), new combination  
*Erythridula styraxae* (Hepner, 1976c:300) (*Erythroneura*), new combination  
*Erythridula tenebrosa* (Knull, 1946a:48) (*Erythroneura*), new combination  
*Erythridula tenuispica* (Beamer, 1930b:444) (*Erythroneura*), new combination  
*Erythridula tietzi* (Ross & DeLong, 1953a:85) (*Erythroneura*), new combination  
*Erythridula tolerata* (Knull, 1951c:180) (*Erythroneura*), new combination  
*Erythridula tomaneki* (Hepner, 1977c:359) (*Erythroneura*), new combination  
*Erythridula tomentosae* (Hepner, 1976c:297) (*Erythroneura*), new combination  
*Erythridula torva* (Beamer, 1935a:98) (*Erythroneura*), new combination  
*Erythridula tridenoides* (Hepner, 1976d:312) (*Erythroneura*), new combination  
*Erythridula tridens* (Beamer, 1930b:450) (*Erythroneura*), new combination  
*Erythridula tura* (Ross & DeLong, 1953a:84) (*Erythroneura*), new combination  
*Erythridula turoides* (Hepner, 1978a:135) (*Erythroneura*), new combination  
*Erythridula ulmalatae* (Ross & DeLong, 1953a:80) (*Erythroneura*), new combination  
*Erythridula ulmarubrae* (Hepner, 1976d:313) (*Erythroneura*), new combination  
*Erythridula ulmosa* (Ross & DeLong, 1953a:78) (*Erythroneura*), new combination  
*Erythridula unicuspidis* (Beamer, 1930b:452) (*Erythroneura*), new combination  
*Erythridula uniforma* (Hepner, 1976d:315) (*Erythroneura*), new combination  
*Erythridula varia* (McAtee, 1920a:287) (*Erythroneura*), new combination  
*Erythridula vartyi* (Hepner, 1977b:51) (*Erythroneura*), new combination  
*Erythridula velutinae* (Hepner, 1977b:51) (*Erythroneura*), new combination  
*Erythridula verae* (Hepner, 1978a:138) (*Erythroneura*), new combination  
*Erythridula verdana* (Ross & DeLong, 1953a:81) (*Erythroneura*), new combination  
*Erythridula victorialis* (Knull, 1946a:49) (*Erythroneura*), new combination  
*Erythridula vierii* (Hepner, 1976b:125) (*Erythroneura*), new combination  
*Erythridula vinaria* (Beamer, 1930b:426) (*Erythroneura*), new combination  
*Erythridula volucris* (Beamer, 1930a:445) (*Erythroneura*), new combination  
*Erythridula wandae* (Hepner, 1976c:299) (*Erythroneura*), new combination  
*Erythridula whitti* (Hepner, 1976b:123) (*Erythroneura*), new combination  
*Erythridula wysongi* (Ross & DeLong, 1953a:84) (*Erythroneura*), new combination  
*Erythridula zephyr* (Ross & DeLong, 1953a:84) (*Erythroneura*), new combination



### *Erythroneura* Fitch

*Erythroneura* Fitch, 1851a:62 (type species:

*E. tricineta* Fitch)

*Erythroneura* (*Erythroneura*) Young 1952:79

**Diagnosis.** Species of the genus can be recognized by the following combination of characters: ground color usually pale, dorsum frequently with bold pattern consisting of oblique lines, transverse bands, or both (Fig. 2-B); forewing usually with dark spot near base of inner apical cell, another near apex of second apical cell, and another on costal margin adjacent to brochosome field; CuA extremely short or absent, base of inner apical cell transverse (Fig. 1-B); male pygofer with dorsal appendage immovably fused, C-shaped (ventral arm of C branched in some species), without additional short internal process at base, ventral appendage absent, ventrolateral setae stout and conspicuous (Fig. 4-B); style apex with three angulate projections; aedeagus usually with

elongate paired basal processes, often with pair of broad flangelike lateral processes distally, denticuli usually indistinct or absent.

**Distribution.** Temperate North America (one species, *E. elegantula* (Osborn), recorded from Panama, an apparent introduction from the United States).

**Notes.** The included species of *Erythroneura* (including *E. calycula* McAtee, which is nearly identical to type species *E. tricineta* for the included characters) were consistently recovered as a monophyletic group in the phylogenetic analysis. The genus is here restricted to equal the definition of the nominotypical subgenus of *Erythroneura* given by Young (1952), which currently comprises 52 valid species. The other three subgenera of *Erythroneura* recognized by Young are here elevated to generic status (see above and below). Most Old World species previously placed in *Erythroneura* have been moved to other genera, but those remaining are here considered *species incertae sedis* (Appendix E).

### Included species:

*Erythroneura aclys* McAtee, 1920a:290  
*Erythroneura acuticephala* Robinson, 1924a:61  
*Erythroneura amanda* McAtee, 1920a:319  
*Erythroneura ancora* Beamer, 1929b:122  
*Erythroneura anfracta* Beamer, 1929b:123  
*Erythroneura aza* Robinson, 1924c:291  
*Erythroneura beameri* Robinson, 1924a:61  
*Erythroneura bidens* McAtee, 1924c:39  
*Erythroneura bistrata* McAtee, 1920a:305  
*Erythroneura caetra* McAtee, 1924d:130  
*Erythroneura calycula* McAtee, 1920a:308  
*Erythroneura cancellata* McAtee, 1920a:320  
*Erythroneura coloradensis* (Gillette, 1892a:16) (*Typhlocyba*)  
*Erythroneura comes* (Say, 1825a:343) (*Tettigonia*)  
*Erythroneura compta* McAtee, 1920a:318  
*Erythroneura corni* Robinson, 1924a:60  
*Erythroneura corona* McAtee, 1920a:304  
*Erythroneura cymbium* McAtee, 1920a:310  
*Erythroneura delicata* McAtee, 1920a:317  
*Erythroneura diva* McAtee, 1920a:308  
*Erythroneura elegans* McAtee, 1920a:315  
*Erythroneura elegantula* Osborn, 1928a:289  
*Erythroneura festiva* Beamer, 1938a:290  
*Erythroneura fiduciaria* Knull, 1951b:170  
*Erythroneura fraxa* Robinson, 1924c:292  
*Erythroneura gilensis* Beamer, 1929b:123

*Erythroneura infuscata* (Gillette, 1898a:764) (*Typhlocyba*)  
*Erythroneura integra* McAtee, 1920a:309  
*Erythroneura kanwakae* Robinson, 1924c:292  
*Erythroneura kennedyi* Knull, 1945b:109  
*Erythroneura maritima* Hamilton, in Hamilton & Langor 1987a:679  
*Erythroneura noncincta* Johnson, 1934a:261  
*Erythroneura nudata* McAtee, 1920a:316  
*Erythroneura octonotata* Walsh, 1862a:149  
*Erythroneura omaska* Robinson, 1924a:62  
*Erythroneura ontari* Robinson, 1924a:60  
*Erythroneura palimpsesta* McAtee, 1924e:43  
*Erythroneura pontifex* McAtee, 1926c:136  
*Erythroneura prima* Beamer, 1938a:264  
*Erythroneura prosata* Johnson, 1935a:108  
*Erythroneura reflecta* McAtee, 1924e:43  
*Erythroneura repetita* McAtee, 1926c:131  
*Erythroneura rosa* Robinson, 1924a:58  
*Erythroneura rubra* (Gillette, 1898a:764) (*Typhlocyba*)  
*Erythroneura rubrella* McAtee, 1920a:316  
*Erythroneura tacita* Beamer, 1938a:293  
*Erythroneura tricincta* Fitch, 1851a:63  
*Erythroneura vaga* Johnson, 1934a:260  
*Erythroneura vagabunda* Knull, 1945b:109  
*Erythroneura vitifex* Fitch, 1856a:392  
*Erythroneura vitis* (Harris, 1831a:43) (*Tettigonia*)  
*Erythroneura ziczac* Walsh, 1862a:149

### ***Eratoneura* Young, new status**

*Erythroneura* (*Eratoneura*) Young 1952:84  
 (type species: *Erythroneura dira*  
 Beamer)

**Diagnosis.** Closely resembling *Erythroneura*, but differing as follows: forewing (Figs. 2-C, 3-B, C) with zigzag pattern usually broken, brown spot of inner apical cell more distinct, second apical cell without dark spot distally, length of vein CuA variable interspecifically; pygofer appendage simple or branched (Fig. 4-C), but not C-shaped, with separate basal internal projection; aedeagal shaft usually without paired basal processes or distal flanges and usually conspicuously denticulate.

**Distribution.** Temperate North America.

**Notes.** Although the phylogenetic analysis re-

covered *Eratoneura* (including *E. ligata* (McAtee), which is nearly identical to type species *E. dira* for the included characters) as paraphyletic with respect to *Erythroneura*, more detailed analyses, including a much larger taxon sample, will be needed to assess more accurately the phylogenetic status of these two genera. Many aspects of the coloration, pygofer structure, and genital morphology of these genera are similar, but all species of *Eratoneura* thus far examined have a unique fingerlike internal process at the base of the pygofer appendage that is absent in all examined species of *Erythroneura*. This possible synapomorphy of *Eratoneura* was outweighed by more homoplastic characters in the analysis. *Eratoneura* currently comprises 308 species. A specimen-level database and interactive key to species are available on-line at [http://ctap.inhs.uiuc.edu/dmitriev/3i\\_keys.asp](http://ctap.inhs.uiuc.edu/dmitriev/3i_keys.asp).

### **Included species:**

*Eratoneura abjecta* (Beamer, 1931d:288) (*Erythroneura*), new combination  
*Eratoneura acantha* (Ross & DeLong, 1950a:296) (*Erythroneura*), new combination  
*Eratoneura accicurta* (Hepner, 1966d:106) (*Erythroneura*), new combination  
*Eratoneura accita* (Knull, 1954b:170) (*Erythroneura*), new combination

*Eratoneura accola* (McAtee, 1920a:299) (*Erythroneura*), new combination  
*Eratoneura acericola* (Ross & DeLong, 1953a:88) (*Erythroneura*), new combination  
*Eratoneura aculeata* (Beamer, 1932g:161) (*Erythroneura*), new combination  
*Eratoneura adunca* (Beamer, 1932c:46) (*Erythroneura*), new combination  
*Eratoneura aesculi* (Beamer, 1932c:46) (*Erythroneura*), new combination  
*Eratoneura affinis* (Fitch, 1851a:63) (*Erythroneura*), new combination  
*Eratoneura albiquera* (Hepner, 1967b:62) (*Erythroneura*), new combination  
*Eratoneura alevra* (Ross, 1956a:89) (*Erythroneura*), new combination  
*Eratoneura alicia* (Ross, 1957a:185) (*Erythroneura*), new combination  
*Eratoneura allecta* (McAtee, 1920a:302) (*Erythroneura*), new combination  
*Eratoneura alloplana* (Ross, 1956a:88) (*Erythroneura*), new combination  
*Eratoneura alveyi* (Hepner, 1972c:269) (*Erythroneura*), new combination  
*Eratoneura amboyensis* (Hepner, 1972a:431) (*Erythroneura*), new combination  
*Eratoneura amethica* (Ross, 1957a:186) (*Erythroneura*), new combination  
*Eratoneura andersoni* (Beamer, 1932e:86) (*Erythroneura*), new combination  
*Eratoneura anseri* (Hepner, 1966d:103) (*Erythroneura*), new combination  
*Eratoneura ardens* (McAtee, 1920a:299) (*Erythroneura*), new combination  
*Eratoneura arenosa* (Ross & DeLong, 1950a:295) (*Erythroneura*), new combination  
*Eratoneura arneri* (Hepner, 1969a:130) (*Erythroneura*), new combination  
*Eratoneura arpegia* (Ross, 1957a:188) (*Erythroneura*), new combination  
*Eratoneura arta* (Beamer, 1931d:287) (*Erythroneura*), new combination  
*Eratoneura asymmetra* (Hepner, 1973a:186) (*Erythroneura*), new combination  
*Eratoneura atkinsoni* (Hepner, 1972c:270) (*Erythroneura*), new combination  
*Eratoneura bainteri* (Hepner, 1972c:271) (*Erythroneura*), new combination  
*Eratoneura ballista* (Beamer, 1932e:84) (*Erythroneura*), new combination  
*Eratoneura basilaris* (Say, 1825a:344) (*Tettigonia*), new combination  
*Eratoneura beeri* (Hepner, 1972c:272) (*Erythroneura*), new combination  
*Eratoneura bella* (McAtee, 1920a:300) (*Erythroneura*), new combination  
*Eratoneura bicurvata* (Hepner, 1973a:184) (*Erythroneura*), new combination  
*Eratoneura bifida* (Beamer, 1931a:134) (*Erythroneura*), new combination  
*Eratoneura bigemina* (McAtee, 1920a:300) (*Erythroneura*), new combination  
*Eratoneura billi* (Hepner, 1966a:88) (*Erythroneura*), new combination  
*Eratoneura biramosa* (Beamer, 1941a:18) (*Erythroneura*), new combination  
*Eratoneura bispinosa* (Beamer, 1931b:241) (*Erythroneura*), new combination  
*Eratoneura blockeri* (Hepner, 1967b:72) (*Erythroneura*), new combination  
*Eratoneura brazzeli* (Hepner, 1966d:106) (*Erythroneura*), new combination  
*Eratoneura brendae* (Hepner, 1967a:21) (*Erythroneura*), new combination  
*Eratoneura brevipes* (Beamer, 1931a:133) (*Erythroneura*), new combination  
*Eratoneura brooki* (Hepner, 1969a:126) (*Erythroneura*), new combination  
*Eratoneura bruceensis* (Hepner, 1975a:6) (*Erythroneura*), new combination  
*Eratoneura byersi* (Hepner, 1972c:271) (*Erythroneura*), new combination  
*Eratoneura caddoensis* (Hepner, 1966b:100) (*Erythroneura*), new combination  
*Eratoneura calamitosa* (Beamer, 1931b:241) (*Erythroneura*), new combination  
*Eratoneura californica* (Beamer, 1932f:143 n.nov.) (*Erythroneura*), new combination  
*Eratoneura callisoga* (Ross, 1956a:86) (*Erythroneura*), new combination  
*Eratoneura campora* (Robinson, 1924a:59) (*Erythroneura*), new combination  
*Eratoneura carmini* (Beamer, 1929b:121) (*Erythroneura*), new combination  
*Eratoneura caverna* (Hepner, 1967a:23) (*Erythroneura*), new combination  
*Eratoneura cavipierra* (Hepner, 1967b:64) (*Erythroneura*), new combination  
*Eratoneura cera* (Hepner, 1966d:105) (*Erythroneura*), new combination  
*Eratoneura certa* (Beamer, 1932g:159) (*Erythroneura*), new combination  
*Eratoneura chehawensis* (Hepner, 1966b:100) (*Erythroneura*), new combination  
*Eratoneura citrosa* (Ross, 1956a:86) (*Erythroneura*), new combination  
*Eratoneura clara* (Beamer, 1932g:161) (*Erythroneura*), new combination



*Eratoneura claroides* (Hepner, 1967a:17) (*Erythroneura*), new combination  
*Eratoneura clavipes* (Beamer, 1931c:269) (*Erythroneura*), new combination  
*Eratoneura codyi* (Hepner, 1966d:101) (*Erythroneura*), new combination  
*Eratoneura colmeri* (Hepner, 1969a:132) (*Erythroneura*), new combination  
*Eratoneura colvardi* (Hepner, 1966b:95) (*Erythroneura*), new combination  
*Eratoneura combesi* (Hepner, 1972c:267) (*Erythroneura*), new combination  
*Eratoneura comoides* (Ross & DeLong, 1953a:90) (*Erythroneura*), new combination  
*Eratoneura compressa* (Knull & Auten, 1937a:573) (*Erythroneura*), new combination  
*Eratoneura concisa* (Beamer, 1931d:286) (*Erythroneura*), new combination  
*Eratoneura confirmata* (McAtee, 1924c:37) (*Erythroneura*), new combination  
*Eratoneura consueta* (Beamer, 1932d:71) (*Erythroneura*), new combination  
*Eratoneura continua* (Knull & Auten, 1937a:578) (*Erythroneura*), new combination  
*Eratoneura contracta* (Beamer, 1931a:130) (*Erythroneura*), new combination  
*Eratoneura corylorubra* (Knull, 1945b:108) (*Erythroneura*), new combination  
*Eratoneura coxi* (Ross & DeLong, 1950a:295) (*Erythroneura*), new combination  
*Eratoneura crinita* (Beamer, 1932e:85) (*Erythroneura*), new combination  
*Eratoneura cristata* (Knull, 1951b:174) (*Erythroneura*), new combination  
*Eratoneura cunninghami* (Hepner, 1966c:3) (*Erythroneura*), new combination  
*Eratoneura curta* (Beamer, 1932e:86) (*Erythroneura*), new combination  
*Eratoneura curtoides* (Hepner, 1972c:272) (*Erythroneura*), new combination  
*Eratoneura curvata* (Beamer, 1931a:132) (*Erythroneura*), new combination  
*Eratoneura custeri* (Hepner, 1966a:89) (*Erythroneura*), new combination  
*Eratoneura daltonorum* (Hepner, 1966a:81) (*Erythroneura*), new combination  
*Eratoneura deformata* (Hepner, 1966a:85) (*Erythroneura*), new combination  
*Eratoneura deklei* (Hepner, 1967a:20) (*Erythroneura*), new combination  
*Eratoneura delongi* (Knull & Auten, 1937a:574) (*Erythroneura*), new combination  
*Eratoneura denmarki* (Hepner, 1967a:20) (*Erythroneura*), new combination  
*Eratoneura dimidiata* (Knull, 1949a:122) (*Erythroneura*), new combination  
*Eratoneura dira* (Beamer, 1931d:286) (*Erythroneura*), new combination  
*Eratoneura direpta* (Knull, 1949a:125) (*Erythroneura*), new combination  
*Eratoneura distincta* (Knull & Auten, 1937a:572) (*Erythroneura*), new combination  
*Eratoneura doeringae* (Hepner, 1975a:7) (*Erythroneura*), new combination  
*Eratoneura douglasi* (Hepner, 1967b:60) (*Erythroneura*), new combination  
*Eratoneura dumosa* (Beamer, 1932a:13) (*Erythroneura*), new combination  
*Eratoneura dura* (Knull, 1954b:170) (*Erythroneura*), new combination  
*Eratoneura econa* (Ross, 1957a:184) (*Erythroneura*), new combination  
*Eratoneura edeni* (Hepner, 1967a:20) (*Erythroneura*), new combination  
*Eratoneura ellisi* (Hepner, 1969a:129) (*Erythroneura*), new combination  
*Eratoneura emquu* (Ross & DeLong, 1953a:88) (*Erythroneura*), new combination  
*Eratoneura era* (McAtee, 1920a:299) (*Erythroneura*), new combination  
*Eratoneura eversi* (Ross & DeLong, 1953a:88) (*Erythroneura*), new combination  
*Eratoneura externa* (Beamer, 1931d:289) (*Erythroneura*), new combination  
*Eratoneura facota* (Beamer, 1932d:70) (*Erythroneura*), new combination  
*Eratoneura fagusae* (Hepner, 1967a:22) (*Erythroneura*), new combination  
*Eratoneura fausta* (Knull, 1951b:172) (*Erythroneura*), new combination  
*Eratoneura fergusonii* (Hepner, 1969a:130) (*Erythroneura*), new combination  
*Eratoneura ferrosa* (Hepner, 1966a:83) (*Erythroneura*), new combination  
*Eratoneura firma* (Beamer, 1932a:12) (*Erythroneura*), new combination  
*Eratoneura flexibilis* (Knull, 1949a:122) (*Erythroneura*), new combination  
*Eratoneura forfex* (Beamer, 1932e:82) (*Erythroneura*), new combination  
*Eratoneura freytagi* (Hepner, 1966a:83) (*Erythroneura*), new combination  
*Eratoneura fulleri* (Hepner, 1967a:19) (*Erythroneura*), new combination  
*Eratoneura gemina* (McAtee, 1920a:301) (*Erythroneura*), new combination  
*Eratoneura gemoides* (Ross, 1953b:190) (*Erythroneura*), new combination

*Eratoneura geronimoi* (Knull, 1945b:108) (*Erythroneura*), new combination  
*Eratoneura gilesi* (Hepner, 1966b:97) (*Erythroneura*), new combination  
*Eratoneura gillettei* (Beamer, 1931a:128) (*Erythroneura*), new combination  
*Eratoneura glicilla* (Ross, 1956a:86) (*Erythroneura*), new combination  
*Eratoneura greeni* (Hepner, 1969a:127) (*Erythroneura*), new combination  
*Eratoneura guiceii* (Hepner, 1972c:269) (*Erythroneura*), new combination  
*Eratoneura hamneri* (Hepner, 1969a:127) (*Erythroneura*), new combination  
*Eratoneura harnedi* (Hepner, 1966c:5) (*Erythroneura*), new combination  
*Eratoneura harpola* (Ross, 1956a:85) (*Erythroneura*), new combination  
*Eratoneura hartii* (Gillette, 1898a:754) (*Typhlocyba*), new combination  
*Eratoneura havana* (Ross & DeLong, 1953a:90) (*Erythroneura*), new combination  
*Eratoneura haysensis* (Hepner, 1966a:79) (*Erythroneura*), new combination  
*Eratoneura hendersoni* (Hepner, 1967a:21) (*Erythroneura*), new combination  
*Eratoneura hepneri* (Dmitriev & Dietrich, 2006a:38 n.nov.) (*Erythroneura*), new combination  
*Eratoneura hibernia* (Hepner, 1966a:83) (*Erythroneura*), new combination  
*Eratoneura hutchinsi* (Hepner, 1966c:2) (*Erythroneura*), new combination  
*Eratoneura hyalina* (Knull & Auten, 1937a:575) (*Erythroneura*), new combination  
*Eratoneura hymac* (Robinson, 1924a:60) (*Erythroneura*), new combination  
*Eratoneura hymettana* (Knull, 1949a:124) (*Erythroneura*), new combination  
*Eratoneura igella* (Ross & DeLong, 1950a:295) (*Erythroneura*), new combination  
*Eratoneura imbricariae* (Ross & DeLong, 1953a:86) (*Erythroneura*), new combination  
*Eratoneura immota* (Beamer, 1932a:16) (*Erythroneura*), new combination  
*Eratoneura impar* (Beamer, 1931a:133) (*Erythroneura*), new combination  
*Eratoneura incondita* (Beamer, 1932a:16) (*Erythroneura*), new combination  
*Eratoneura inepta* (Beamer, 1932g:162) (*Erythroneura*), new combination  
*Eratoneura ingrata* (Beamer, 1932g:160) (*Erythroneura*), new combination  
*Eratoneura inksana* (Knull, 1954b:170) (*Erythroneura*), new combination  
*Eratoneura interna* (Beamer, 1931d:285) (*Erythroneura*), new combination  
*Eratoneura johnsoni* (Hepner, 1972a:432) (*Erythroneura*), new combination  
*Eratoneura kansana* (Baker, 1925b:537 n.nov.) (*Erythroneura*), new combination  
*Eratoneura kirki* (Hepner, 1967b:64) (*Erythroneura*), new combination  
*Eratoneura knighti* (Beamer, 1932e:87) (*Erythroneura*), new combination  
*Eratoneura knullae* (Ross, 1953b:192) (*Erythroneura*), new combination  
*Eratoneura krameri* (Hepner, 1967b:67) (*Erythroneura*), new combination  
*Eratoneura kuiterti* (Hepner, 1967a:17) (*Erythroneura*), new combination  
*Eratoneura lamucata* (Ross & DeLong, 1953a:88) (*Erythroneura*), new combination  
*Eratoneura larryi* (Hepner, 1966a:89) (*Erythroneura*), new combination  
*Eratoneura lata* (Beamer, 1932e:86) (*Erythroneura*), new combination  
*Eratoneura lawsoni* (Robinson, 1924a:59) (*Erythroneura*), new combination  
*Eratoneura lenta* (Beamer, 1932e:82) (*Erythroneura*), new combination  
*Eratoneura levecki* (Hepner, 1966b:99) (*Erythroneura*), new combination  
*Eratoneura ligata* (McAtee, 1920a:301) (*Erythroneura*), new combination  
*Eratoneura lillianae* (Hepner, 1966a:89) (*Erythroneura*), new combination  
*Eratoneura linea* (Beamer, 1932c:47) (*Erythroneura*), new combination  
*Eratoneura longa* (Knull, 1955a:245) (*Erythroneura*), new combination  
*Eratoneura longifurca* (Hepner, 1966c:3) (*Erythroneura*), new combination  
*Eratoneura lorae* (Hepner, 1967b:70) (*Erythroneura*), new combination  
*Eratoneura lucora* (Hepner, 1967a:24) (*Erythroneura*), new combination  
*Eratoneura luculenta* (Knull, 1949a:124) (*Erythroneura*), new combination  
*Eratoneura lucyae* (Hepner, 1966a:81) (*Erythroneura*), new combination  
*Eratoneura lunata* (McAtee, 1924e:41) (*Erythroneura*), new combination  
*Eratoneura lundi* (Hepner, 1967a:22) (*Erythroneura*), new combination  
*Eratoneura lyriquera* (Hepner, 1967b:61) (*Erythroneura*), new combination  
*Eratoneura macra* (Beamer, 1932a:15) (*Erythroneura*), new combination

*Eratoneura maculata* (Gillette, 1898a:764) (*Typhlocyba*), new combination  
*Eratoneura maga* (Knull, 1951b:170) (*Erythroneura*), new combination  
*Eratoneura malaca* (Knull, 1949a:126) (*Erythroneura*), new combination  
*Eratoneura manus* (Beamer, 1932e:83) (*Erythroneura*), new combination  
*Eratoneura marilandicae* (Ross, 1957a:183) (*Erythroneura*), new combination  
*Eratoneura mariquera* (Hepner, 1973a:186) (*Erythroneura*), new combination  
*Eratoneura marra* (Beamer, 1932g:160) (*Erythroneura*), new combination  
*Eratoneura massonae* (Knull, 1954b:171) (*Erythroneura*), new combination  
*Eratoneura maxwelli* (Hepner, 1972b:218) (*Erythroneura*), new combination  
*Eratoneura meadi* (Hepner, 1966a:79) (*Erythroneura*), new combination  
*Eratoneura mensa* (Beamer, 1931d:287) (*Erythroneura*), new combination  
*Eratoneura metopia* (Ross, 1957a:185) (*Erythroneura*), new combination  
*Eratoneura micheneri* (Hepner, 1972c:271) (*Erythroneura*), new combination  
*Eratoneura millsii* (Ross & DeLong, 1950a:291) (*Erythroneura*), new combination  
*Eratoneura mimica* (Ross, 1957a:190) (*Erythroneura*), new combination  
*Eratoneura minor* (Beamer, 1932e:84) (*Erythroneura*), new combination  
*Eratoneura mira* (Beamer, 1932c:45) (*Erythroneura*), new combination  
*Eratoneura mirifica* (Beamer, 1932d:159) (*Erythroneura*), new combination  
*Eratoneura misera* (Beamer, 1932g:158) (*Erythroneura*), new combination  
*Eratoneura morgani* (DeLong, 1916a:104) (*Typhlocyba*), new combination  
*Eratoneura natchezensis* (Hepner, 1967b:70) (*Erythroneura*), new combination  
*Eratoneura nevadensis* (Beamer, 1932d:72) (*Erythroneura*), new combination  
*Eratoneura nielsoni* (Hepner, 1967b:62) (*Erythroneura*), new combination  
*Eratoneura nigriquera* (Hepner, 1967b:60) (*Erythroneura*), new combination  
*Eratoneura nigriventer* (Beamer, 1931a:134) (*Erythroneura*), new combination  
*Eratoneura nimia* (Knull, 1954b:171) (*Erythroneura*), new combination  
*Eratoneura noncuspidis* (Beamer, 1931a:129) (*Erythroneura*), new combination  
*Eratoneura norica* (Ross, 1956a:88) (*Erythroneura*), new combination  
*Eratoneura omani* (Beamer, 1930a:49) (*Erythroneura*), new combination  
*Eratoneura opulenta* (Beamer, 1932c:48) (*Erythroneura*), new combination  
*Eratoneura osborni* (DeLong, 1916a:103) (*Typhlocyba*), new combination  
*Eratoneura ostryae* (Hepner, 1967a:23) (*Erythroneura*), new combination  
*Eratoneura pallida* (Knull & Auten, 1937a:573) (*Erythroneura*), new combination  
*Eratoneura paluloides* (Ross, 1953b:189) (*Erythroneura*), new combination  
*Eratoneura pamela* (Hepner, 1967b:67) (*Erythroneura*), new combination  
*Eratoneura paraesculi* (Knull, 1945b:106) (*Erythroneura*), new combination  
*Eratoneura parallela* (McAtee, 1924c:38) (*Erythroneura*), new combination  
*Eratoneura parisensis* (Hepner, 1972a:431) (*Erythroneura*), new combination  
*Eratoneura parva* (Beamer, 1932d:70) (*Erythroneura*), new combination  
*Eratoneura parvipes* (Beamer, 1931b:242) (*Erythroneura*), new combination  
*Eratoneura patei* (Hepner, 1967a:19) (*Erythroneura*), new combination  
*Eratoneura patriciae* (Hepner, 1966a:88) (*Erythroneura*), new combination  
*Eratoneura patris* (Ross & DeLong, 1953a:89) (*Erythroneura*), new combination  
*Eratoneura paulae* (Hepner, 1966a:81) (*Erythroneura*), new combination  
*Eratoneura penerostrata* (Beamer, 1932e:85) (*Erythroneura*), new combination  
*Eratoneura penesica* (Beamer, 1931c:269) (*Erythroneura*), new combination  
*Eratoneura perplexa* (Knull, 1944b:123 n.nov.) (*Erythroneura*), new combination  
*Eratoneura phellos* (Ross & DeLong, 1953a:90) (*Erythroneura*), new combination  
*Eratoneura pitrei* (Hepner, 1973a:184) (*Erythroneura*), new combination  
*Eratoneura priniquera* (Hepner, 1967b:68) (*Erythroneura*), new combination  
*Eratoneura prolixa* (Knull, 1949a:126) (*Erythroneura*), new combination  
*Eratoneura propria* (Beamer, 1932a:13) (*Erythroneura*), new combination  
*Eratoneura protuma* (Ross, 1957a:188) (*Erythroneura*), new combination  
*Eratoneura pumicasta* (Hepner, 1967b:72) (*Erythroneura*), new combination



*Eratoneura pyra* (McAtee, 1924d:133) (*Erythroneura*), new combination  
*Eratoneura quercalbae* (Ross & DeLong, 1950a:294) (*Erythroneura*), new combination  
*Eratoneura rangifer* (Ross & DeLong, 1950a:292) (*Erythroneura*), new combination  
*Eratoneura ratcliffensis* (Hepner, 1966a:85) (*Erythroneura*), new combination  
*Eratoneura reedi* (Hepner, 1967b:61) (*Erythroneura*), new combination  
*Eratoneura reiteri* (Hepner, 1966a:87) (*Erythroneura*), new combination  
*Eratoneura restricta* (Beamer, 1932c:45) (*Erythroneura*), new combination  
*Eratoneura retusa* (Beamer, 1932c:48) (*Erythroneura*), new combination  
*Eratoneura richardsi* (Ross, 1953b:189) (*Erythroneura*), new combination  
*Eratoneura robinsoni* (Hepner, 1966a:89) (*Erythroneura*), new combination  
*Eratoneura robusta* (Knull, 1955a:245) (*Erythroneura*), new combination  
*Eratoneura rossi* (Hepner, 1966a:85) (*Erythroneura*), new combination  
*Eratoneura rostrata* (Beamer, 1931c:270) (*Erythroneura*), new combination  
*Eratoneura rotunda* (Beamer, 1931d:288) (*Erythroneura*), new combination  
*Eratoneura rubida* (Knull, 1954b:171) (*Erythroneura*), new combination  
*Eratoneura rubranotata* (Beamer, 1927a:30) (*Erythroneura*), new combination  
*Eratoneura rubraria* (Hepner, 1967b:66) (*Erythroneura*), new combination  
*Eratoneura rubraza* (Robinson, 1924c:291) (*Erythroneura*), new combination  
*Eratoneura rubulna* (Hepner, 1972a:433) (*Erythroneura*), new combination  
*Eratoneura sadleri* (Hepner, 1969a:132) (*Erythroneura*), new combination  
*Eratoneura sancta* (Beamer, 1932a:15) (*Erythroneura*), new combination  
*Eratoneura sanctaerosae* (Hepner, 1967a:24) (*Erythroneura*), new combination  
*Eratoneura sandersoni* (Ross, 1956a:90) (*Erythroneura*), new combination  
*Eratoneura schista* (Knull, 1955a:246) (*Erythroneura*), new combination  
*Eratoneura scobyensis* (Hepner, 1966b:97) (*Erythroneura*), new combination  
*Eratoneura sebringensis* (Hepner, 1966b:97) (*Erythroneura*), new combination  
*Eratoneura separata* (Beamer, 1932a:12) (*Erythroneura*), new combination  
*Eratoneura septima* (Beamer, 1927a:30) (*Erythroneura*), new combination  
*Eratoneura sethi* (Hepner, 1966b:100) (*Erythroneura*), new combination  
*Eratoneura severini* (Knull, 1949a:125) (*Erythroneura*), new combination  
*Eratoneura shumiquera* (Hepner, 1972a:431) (*Erythroneura*), new combination  
*Eratoneura siloamensis* (Hepner, 1967a:22) (*Erythroneura*), new combination  
*Eratoneura smithi* (Ross, 1956a:90) (*Erythroneura*), new combination  
*Eratoneura socia* (Knull, 1954b:171) (*Erythroneura*), new combination  
*Eratoneura solida* (Knull, 1954b:171) (*Erythroneura*), new combination  
*Eratoneura solita* (Beamer, 1932a:14) (*Erythroneura*), new combination  
*Eratoneura sorota* (Hepner, 1975a:5) (*Erythroneura*), new combination  
*Eratoneura spala* (Ross & DeLong, 1950a:294) (*Erythroneura*), new combination  
*Eratoneura spinea* (Knull, 1951b:172) (*Erythroneura*), new combination  
*Eratoneura spinifera* (Beamer, 1931b:240) (*Erythroneura*), new combination  
*Eratoneura spiniterma* (Hepner, 1969a:133) (*Erythroneura*), new combination  
*Eratoneura staffordi* (Hepner, 1966c:3) (*Erythroneura*), new combination  
*Eratoneura staminea* (Knull, 1954b:171) (*Erythroneura*), new combination  
*Eratoneura stannardi* (Hepner, 1967b:66) (*Erythroneura*), new combination  
*Eratoneura starksvillensis* (Hepner, 1966d:103) (*Erythroneura*), new combination  
*Eratoneura stephensoni* (Beamer, 1931a:130) (*Erythroneura*), new combination  
*Eratoneura stoveri* (Ross & DeLong, 1950a:296) (*Erythroneura*), new combination  
*Eratoneura stupkaorum* (Knull, 1945b:104) (*Erythroneura*), new combination  
*Eratoneura tammina* (Ross & DeLong, 1953a:86) (*Erythroneura*), new combination  
*Eratoneura tantilla* (Beamer, 1931d:285) (*Erythroneura*), new combination  
*Eratoneura tantula* (Knull, 1954b:171) (*Erythroneura*), new combination  
*Eratoneura tenilla* (Ross & DeLong, 1950a:294) (*Erythroneura*), new combination  
*Eratoneura tenuitas* (Knull, 1954b:173) (*Erythroneura*), new combination  
*Eratoneura teres* (Beamer, 1931c:268) (*Erythroneura*), new combination

*Eratoneura tersa* (Knull, 1951b:172) (*Erythroneura*), new combination  
*Eratoneura teshi* (Hepner, 1972c:267) (*Erythroneura*), new combination  
*Eratoneura texana* (Beamer, 1929b:121) (*Erythroneura*), new combination  
*Eratoneura thaxtoni* (Hepner, 1966c:2) (*Erythroneura*), new combination  
*Eratoneura torella* (Robinson, 1924b:156) (*Erythroneura*), new combination  
*Eratoneura trautmanae* (Knull, 1945b:104) (*Erythroneura*), new combination  
*Eratoneura triangulata* (Beamer, 1931b:240) (*Erythroneura*), new combination  
*Eratoneura trivittata* (Robinson, 1924a:59) (*Erythroneura*), new combination  
*Eratoneura tumida* (Knull, 1954b:173) (*Erythroneura*), new combination  
*Eratoneura turgida* (Beamer, 1931b:243) (*Erythroneura*), new combination  
*Eratoneura unca* (Knull, 1954b:174) (*Erythroneura*), new combination  
*Eratoneura uncinata* (Beamer, 1931b:242) (*Erythroneura*), new combination  
*Eratoneura unguilata* (Beamer, 1932d:69) (*Erythroneura*), new combination  
*Eratoneura unica* (Beamer, 1932e:83) (*Erythroneura*), new combination  
*Eratoneura univittata* (Robinson, 1924b:156) (*Erythroneura*), new combination  
*Eratoneura usitata* (Beamer, 1932a:14) (*Erythroneura*), new combination  
*Eratoneura uvaldeana* (Knull, 1949a:125) (*Erythroneura*), new combination  
*Eratoneura vacua* (Knull, 1954b:174) (*Erythroneura*), new combination  
*Eratoneura valida* (Knull, 1954b:174) (*Erythroneura*), new combination  
*Eratoneura velox* (Ross, 1953b:190) (*Erythroneura*), new combination  
*Eratoneura ventura* (Knull & Auten, 1937a:577) (*Erythroneura*), new combination  
*Eratoneura vinsoni* (Hepner, 1969a:129) (*Erythroneura*), new combination  
*Eratoneura vittata* (Knull & Auten, 1937a:577) (*Erythroneura*), new combination  
*Eratoneura vulgaris* (Hepner, 1975a:4) (*Erythroneura*), new combination  
*Eratoneura weemsi* (Hepner, 1967a:19) (*Erythroneura*), new combination  
*Eratoneura whitcombi* (Hepner, 1975a:6) (*Erythroneura*), new combination  
*Eratoneura wilsoni* (Hepner, 1966d:106) (*Erythroneura*), new combination  
*Eratoneura winslowensis* (Hepner, 1966a:85) (*Erythroneura*), new combination  
*Eratoneura wisei* (Hepner, 1966b:97) (*Erythroneura*), new combination  
*Eratoneura wiyguli* (Hepner, 1966d:103) (*Erythroneura*), new combination  
*Eratoneura wolcottensis* (Hepner, 1973a:185) (*Erythroneura*), new combination  
*Eratoneura woodruffi* (Hepner, 1967a:23) (*Erythroneura*), new combination  
*Eratoneura youngi* (Hepner, 1966a:87) (*Erythroneura*), new combination  
*Eratoneura zioni* (Beamer, 1932d:71) (*Erythroneura*), new combination

### *Erasmoneura* Young, new status

*Erythroneura* (*Erasmoneura*) Young 1952:80  
 (type species: *Erythroneura vulnerata* Fitch)

**Diagnosis.** Resembling *Erythroneura* in having third point on male style, but differing as follows: coloration usually darker overall; head usually more strongly produced (Fig. 2-D); base of forewing inner apical cell angulate and lacking distinct brown spot (Fig. 3-D); pygofer appendage separated from margin by a basal line of weakening (Fig. 4-D); aedeagus with preatrium elongate, with pair of apical or preapical spines or processes, without elongate basal processes.

**Distribution.** Temperate North America; introduced into southern Europe (Duso, et al. 2005).

**Notes.** Phylogenetic analysis of morphological characters placed the included species of *Erasmoneura* as monophyletic sister to the *Erythroneura* + *Eratoneura* clade, justifying the elevation of *Erasmoneura* to generic rank. Three species formerly included in *Erasmoneura* are here removed and placed in a separate new genus, *Rossmoneura*, described below based on differences in coloration, the structure of the head, and the structure of the aedeagus. *Erasmoneura* currently comprises 12 valid species. A specimen-level database and interactive key to species are available on-line at [http://ctap.inhs.uiuc.edu/dmitriev/3i\\_keys.asp](http://ctap.inhs.uiuc.edu/dmitriev/3i_keys.asp).

**Included species:**

*Erasmoneura atrata* (Johnson, 1935a:97) (*Erythroneura*), new combination  
*Erasmoneura bicolorata* (Beamer, 1937a:11) (*Erythroneura*), new combination  
*Erasmoneura bipentagona* (Beamer, 1927a:31) (*Erythroneura*), new combination  
*Erasmoneura caerulea* (Beamer, 1937a:10) (*Erythroneura*), new combination  
*Erasmoneura fulmina* (McAtee, 1920a:274) (*Erythroneura*), new combination  
*Erasmoneura gradata* (Robinson, 1924a:58) (*Erythroneura*), new combination  
*Erasmoneura mixta* (Beamer, 1932j:183) (*Erythroneura*), new combination  
*Erasmoneura nigerrima* (McAtee, 1920a:275) (*Erythroneura*), new combination  
*Erasmoneura nigra* (Gillette, 1898a:765) (*Typhlocyba*), new combination  
*Erasmoneura rubricata* (Van Duzee, 1909a:229) (*Typhlocyba*), new combination  
*Erasmoneura variabilis* (Beamer, 1929b:126) (*Erythroneura*), new combination  
*Erasmoneura vulnerata* (Fitch, 1851a:62) (*Erythroneura*), new combination

***Hymetta* McAtee**

*Hymetta* McAtee 1919:121 (type species:  
*Tettigonia trifasciata* Say)

**Diagnosis.** This small, distinctive genus is characterized by the following combination of features: head pale, without dark spots on face or crown; scutellum elevated posteriorly, apex black; forewing broad, marked with numerous small irregular reddish or brownish flecks (Fig. 2-E); pygofer with dorsal appendage immov-

ably fused to margin, ventral appendage absent, basolateral setal group well differentiated (Fig. 4-E); style apex footlike without third point.

**Distribution.** Temperate North America.

**Notes.** Phylogenetic analysis supported the monophyly of *Hymetta* and placed the genus as sister to *Illinigina*, n. gen. *Hymetta* currently comprises six valid species. A specimen-level database and interactive key to species are available on-line at [http://ctap.inhs.uiuc.edu/dmitriev/3i\\_keys.asp](http://ctap.inhs.uiuc.edu/dmitriev/3i_keys.asp).

**Included species:**

*Hymetta anthisma* McAtee, 1919a: 123  
*Hymetta arizoniana* Fairbairn, 1928a: 90  
*Hymetta balteata* McAtee, 1919a: 123  
*Hymetta distincta* Fairbairn, 1928a: 87  
*Hymetta kansasensis* Fairbairn, 1928a: 90  
*Hymetta trifasciata* (Say, 1825a: 343) (*Tettigonia*)

**Descriptions of New Taxa  
North American Genera*****Aztegina*, new genus**

(Figs. 2-F; 3-F, V; 4-F; 6-A-E; 11-A, O)

**Type species:** *Aztegina punctinota*, new species, here designated.

**Diagnosis.** Length 3.1–3.3mm. Color pale yellow with brown markings; head with small median apical spot; mesonotal triangles dark brown; apex of scutellum black; forewing symmetrically marked with brown but without distinct pattern (Fig. 2-F). Head narrower than pronotum; crown angulately produced, longer medially than next to eye, coronal suture complete. Scutellum not elevated apically. Forewing (Fig. 3-F) with inner apical

cell base oblique, length of CuA subequal to that of CuP; third apical cell slender, parallel-sided; outer apical cell less than 2X longer than wide; anal vein moderately well delimited. Hindwing (Fig. 3-V) vein RA present; m-cu crossvein absent, CuA confluent with MP for short distance. Sternite IX without median internal ridge. Pygofer (Figs. 4-F, 11-O) with broad dorsal emargination not extended to base; without oblique dorsolateral internal ridge; surface with conspicuous microtrichia distally, sparse fine setae basolaterally; basolateral setal group undifferentiated; apical lobe with group of short fine setae on mesal surface; dorsal appendage rigidly attached to pygofer margin, slender, upturned distally; ventral appendage absent; unsclerotized areas restricted to margin. First segment of anal tube with basolateral arm well developed, connected by membrane to



pygofer just ventrad of dorsal appendage base, microtrichia inconspicuous. Subgenital plate (Fig. 6-A) with basolateral angle acute; without conspicuous dorsal fold; submarginal row with three macrosetae; marginal row with short peg-like setae basally and short fine setae distally; distal lobe weakly expanded. Connective (Fig. 6-D) V-shaped, without stem or median keel. Style (Fig. 6-E) preapical lobe large, truncate; apophysis short, footlike, with imbricate texture. Aedeagus (Figs. 6-B, C) without preatrium; dorsal apodeme long, narrow, weakly expanded dorsally, apex T-shaped in posterior view, connections to pygofer membranous; shaft elongate with short paired apical processes; gonopore subapical on posterior surface.

**Distribution.** Mexico.

**Notes.** The genus name, which is feminine, combines "Aztec" the indigenous people who inhabited the vicinity of present-day Mexico City prior to the arrival of the Spanish conquistadors, with "*Zygina*" a genus of Erythroneurini. The genus is based on a single new species recorded from Mexico. In the phylogenetic analysis, this species was consistently placed as sister to a clade comprising the New World genera *Mexigina*, *Neozygina*, *Hepzygina*, and *Zyginama*.

#### Included species:

*Aztegina punctinota*, n. sp.

#### *Aztegina punctinota*, new species

**Type locality:** Distrito Federal, Mexico

**Diagnosis.** Length of male 3.1mm, female 3.3mm. Ground color yellow-green; crown midline, two large sublateral pronotal spots, two maculae on either end of forewing brochosome field, and mesosternum dark brown. Forewing with diffuse transcommisural diamond-shaped brown mark in basal half, distal third infused with brown; metathorax except legs and wings bright orange. Male abdominal 2S apodemes relatively narrow, extended to posterior margin of sternite III (Fig. 11-A). Genital capsule, connective, and styles as described for genus; aedeagus with shaft in posterior view (Fig. 6-C) bearing pair of rounded lateroapical lobes; pair of slender processes arising distad of gonopore extended anterolaterad.

**Material examined.** Holotype ♂: MEXICO: DF: rt. 95 km 41 S. Mexico City, 2970m,

N19.12496, W99.19440, 18-X-2005, C. H. Dietrich, MX05-03-2, sweeping; 6 ♂♂ and 4 ♀♀ paratypes, same data [INHS]. Other material: 1 ♂, MEXICO: DF: Mexico City, 13-IX-1939, D. M. DeLong [INHS].

#### *Hepzygina*, new genus

(Figs. 2-G; 3-G; 4-G; 6-F, G)

**Type species:** *Erythroneura milleri* Beamer, here designated

**Diagnosis.** Length 2.3–3mm. Color pale overall with various orange and brown markings; head with or without small apical brown spot and pair of indistinct preapical orange or brown spots on crown (Fig. 2-G). Head slightly narrower than pronotum; crown angulately produced, slightly longer medially than next to eyes, coronal suture complete. Wing venation (Fig. 3-G) as in *Aztegina*. Sternite IX with median internal ridge anteriorly. Pygofer (Fig. 4-G) broadly emarginate dorsally to near base; without oblique dorsolateral internal ridge; surface with distinct microtrichia and scattered fine setae; basolateral setal group well developed with several moderately large setae; apical lobe with group of short slender setae on mesal surface; dorsal appendage elongate, straight or slightly sinuate, rigidly attached to pygofer margin; ventral appendage absent; posteroventral area weakly sclerotized. First segment of anal tube with basolateral arm well developed, straight, articulated near pygofer dorsal margin; microtrichia inconspicuous. Subgenital plate with basolateral angle acute; without conspicuous dorsal fold; submarginal row with three macrosetae; marginal row continuous from base to apex, with microsetae short and slender; distal lobe not expanded. Connective U-shaped; stem broad, bifid, depressed, overlapping base of aedeagus. Style preapical lobe very large; apophysis short, smooth, truncate, with two points. Aedeagus (Figs. 6-F, G) with preatrium short; dorsal apodeme short, compressed, expanded anterad in lateral view, with pair of posterolateral lobes, connections to pygofer membranous; shaft compressed with elongate recurved median ventral process arising near base, paired distal processes absent.

**Distribution.** Southwestern USA and Mexico.

**Notes.** Phylogenetic analysis recovered the two included species as a monophyletic sister group to *Zyginama*, n. gen. The genus name,

which is feminine, was formed by combining the first syllable of the surname of Dr. Leon Hepner, who described many of the New World Erythroneurini, with *Zygina*, the genus in which the type species was previously placed. This genus is described based on two species previously included by Young (1952) in the "Ritana group" of *Zygina*. Examination of the female holotype of *Erythroneura tergemina* Van Duzee

(California Academy of Sciences) reveals that it is a synonym of *H. aprica* (McAtee). Both names were published in the same year, but the latter appears to have priority. A few Mexican specimens of this genus in the INHS collection differ somewhat from the previously described species in the structure of the aedeagus and may represent morphological variants or undescribed species.

### Included species:

*Hepzygina aprica* (McAtee, 1924d:132) (*Erythroneura*), new combination

*Erythroneura tergemina* Van Duzee, 1924a:235, new synonym

*Hepzygina milleri* (Beamer, 1929b:125) (*Erythroneura*), new combination

### *Illinigina*, new genus

(Figs. 2-H; 3-H, W; 4-H, 6-I-L)

**Type species:** *Erythroneura illinoiensis* Gillette, here designated.

**Diagnosis.** Length 2.8–3.2mm. Overall color pale yellow, with median red or brown spots on pronotum, scutellum, and sometimes crown; forewing with few symmetrical brown spots or maculae in basal half, apical cells unmarked (Fig. 2-H). Head slightly narrower than pronotum; crown angulately produced, longer medially than next to eye. Scutellum not elevated apically. Forewing (Fig. 3-H) with inner apical cell base oblique, length of CuA subequal to that of CuP; third apical cell relatively broad, slightly widened distally; outer apical cell approximately 2X longer than wide; anal vein obsolete. Hindwing (Fig. 3-W) with vein RA present; m-cu very short, CuA and MP nearly touching at one point. Sternite IX with median longitudinal internal ridge anteriorly. Pygofer (Fig. 4-H) with narrow dorsal emargination extended to base; dorsolateral oblique internal ridge present; surface sparsely clothed with fine setae, microtrichia inconspicuous; basolateral setal group present but poorly differentiated; apical lobe with group of short slender setae on mesal surface; dorsal appendage short, tapered, upturned, movably articulated to dorsal margin of pygofer, connected to dorsal apodeme of aedeagus by well-sclerotized ligament (Figs. 6-I, J); ventral appendage absent; unsclerotized areas restricted to ventral margin. First segment of anal tube with basolateral arm poorly developed, microtrichia inconspicuous. Subgenital plate (Fig. 4H) with basolateral angle acute;

dorsal fold angulate; submarginal row with 3–4 macrosetae; marginal row with short, fine setae; distal lobe weakly expanded. Connective (Fig. 6-K) Y-shaped; stem short, compressed. Style (Fig. 6L) preapical lobe well developed, oblique; apophysis short, smooth, apex hatchet-like, with two points. Aedeagus (Figs. 6-I, J) with preatrium well developed; dorsal apodeme well developed, somewhat expanded in lateral view; shaft short, compressed, with pair of slender basal processes; gonopore terminal.

**Distribution.** Temperate North America.

**Notes.** The genus name, which is feminine, is derived in part from the name of its only included species, which in turn is based on the type locality. The only known species of the genus, *I. illinoiensis*, was sister to *Hymetta* in the phylogenetic analysis. These two genera have the dorsal appendage of the pygofer very similar in shape, both lack a second extension on the male style apex, and both have the scutellum apex darkly pigmented, in contrast to the rest of the scutellum. *Illinigina* differs from *Hymetta* in having the forewings more slender and lacking red flecks and transverse bands, and the scutellum not elevated posteriorly. *I. illinoiensis* is widespread and somewhat variable in coloration (two named color forms, *regalis* Beamer and *spectra* McAtee are considered synonyms of *I. illinoiensis*) but is readily distinguished from other New World Erythroneurini by the distinctive pattern of red and brown spots on the scutellum, forewing, and usually also the head and pronotum.



**Included species:**

*Illinigina illinoiensis* (Gillette, 1898a:758) (*Typhlocyba*), new combination

*Erythroneura illinoiensis* var. *regalis* Beamer 1929b:125, new synonym

*Erythroneura illinoiensis* var. *spectra* McAtee 1920a:292, new synonym

***Mexigina*, new genus**

(Figs. 1-A, D; 2-I; 3-I, X; 4-I; 6-M–P; 11-B)

**Type species:** *Erythroneura oculata* McAtee, here designated.

**Diagnosis.** Length 2.5–2.7mm. Dorsal coloration (Fig. 2-I) mostly dark brown; head pale with two pairs of preapical brown spots, one on crown, one more widely separated just dorsad of antennal pits (Fig. 1-A). Mesonotal triangles dark brown, apex of scutellum pale. Forewing (Fig. 3-I) heavily infused with fuscous, without distinct pattern; inner apical cell base oblique, length of CuA subequal to that of CuP; third apical cell broadened distally; outer apical cell approximately 2X longer than wide; anal vein poorly delimited. Hind wing vein RA absent; m-cu crossvein absent, CuA confluent with MP for short distance. Sternite IX with median longitudinal internal ridge anteriorly. Pygofer (Fig. 4-I) broadly emarginate to base dorsally; without dorsolateral oblique ridge; surface with distinct microtrichia, fine setae sparse; basolateral setal group well differentiated, setae somewhat enlarged; apical lobe with group of short slender setae near margin; dorsal margin

strongly sclerotized but without appendage; ventral appendage well developed; membranous areas restricted to margin. First segment of anal tube with basolateral arm well developed, expanded distally, articulated to pygofer margin; microtrichia indistinct. Subgenital plate (Fig. 4-I) with basolateral angle acute; without conspicuous dorsal fold; submarginal row with 3–4 macrosetae; marginal row with setae short and slender, very sparse distally; distal lobe not expanded. Connective U-shaped; stem short, compressed into dorsal keel. Style (Fig. 6-P) with preapical lobe large, truncate; apophysis short, smooth, footlike. Aedeagus (Figs. 6-M, N) without preatrium; dorsal apodeme slender, T-shaped in posterior view, connections to pygofer membranous; shaft compressed, with pair of lamelliform apical processes; gonopore preapical on posterior surface.

**Distribution.** Southwestern USA and Mexico.

**Notes.** This is the only North American erythroneurine genus known to lack a dorsal pygofer appendage. The only known species is *M. oculata* (McAtee), which was included by Young (1952) in the “*ritana* group” of *Zygina*. The genus name, which is feminine, refers to the primarily Mexican distribution of the type species.

**Included species:**

*Mexigina oculata* (McAtee, 1924e:39) (*Erythroneura*), new combination

***Nelionidia*, new genus**

(Figs. 2-J; 3-K–M, Z; 4-K–M; 7-A–O; 1-D, Q–S)

**Type species:** *N. pueblensis*, new species, here designated.

**Diagnosis.** Length 2.5–3.3mm. Ground color pale yellow, variously marked with brown, head with pair of preapical brown spots on crown (Fig. 2-J). Head slightly narrower than pronotum; crown produced, slightly longer medially than next to eye, coronal suture complete. Forewing (Figs. 3-K–M) inner apical cell base angulate; CuA shorter than CuP, subequal to basal segment of MP; third apical cell widened distally; outer apical cell usually

twice as long as wide. Hindwing (Fig. 3Z) vein RA weakly delimited; MP and CuA confluent for short distance. Sternite IX without median internal ridge. Pygofer (Figs. 4-J–M; 11-Q–S) weakly to strongly emarginate dorsally; oblique dorsolateral internal ridge weakly to strongly developed; surface with distinct microtrichia, without fine setae; basolateral setal group well delimited with several setae; apical lobe with distinct group of short slender setae on inner surface; dorsal appendage usually curved ventrad then posterad, articulated to pygofer side, anteroventral lobe connected by well-sclerotized tendon to dorsal apodeme of aedeagus; ventral appendage absent. First segment of anal tube with basolateral arm weakly sclerotized, extended to junction of aedeagal tendon



and pygofer appendage; microtrichia inconspicuous. Subgenital plate (Figs. 4J-M) with basolateral angle obtuse; without conspicuous dorsal fold; submarginal row with three macrosetae; marginal row with microsetae short and slender, continuous from subbasal angle to near apex. Connective (Fig. 7-D) broadly U-shaped; stem short, compressed. Style (Fig. 7-C) preapical lobe prominent but not greatly enlarged; apophysis smooth, with three points or angles of various sizes. Aedeagus (Figs. 7-A, B) with preatrium short or absent; dorsal apodeme in lateral view long, narrow, compressed; shaft elongate, slender, with pair of long recurved processes apically, gonopore apical or subapical on posterior surface. Fe-

male sternite VII with posterior margin acutely produced, process weakly constricted.  
**Distribution.** Mexico.  
**Notes.** The genus name, which is feminine, is a modification of that of the superficially similar Eremian genus *Helionidia* Zachvatkin, which differs in having a distinctive style and the connective with a median anterior lobe. *Nelionidia* is described based on four new species from Mexico and one previously described species, *Erythroneura amicus* Ross. The latter was not selected as the type species because its dorsal pygofer appendage differs considerably from that of other species in the genus, and because only a single specimen is known.

**Included species:**

- Nelionidia amicus* (Ross, 1965:268) (*Erythroneura*), new combination
- Nelionidia elliptica*, n. sp.
- Nelionidia moyai*, n. sp.
- Nelionidia pallescens*, n. sp.
- Nelionidia pueblensis*, n. sp.

**Key to Males of *Nelionidia***

- 1 Dorsum nearly uniformly pale yellow except pair of brown preapical spots on crown; aedeagus without anteriorly projecting subapical spine (Fig. 7-H) .....*pallescens*, n. sp.  
1' Dorsum heavily marked with dark brown (Fig. 2-J); aedeagus with anteriorly projecting subapical spine (Figs. 7-A, E, L) .....2
- 2 Pygofer with posteromedial emargination constricted and parallel-sided in basal half; style apex with third point elongate, approximately as long as distance between first and second points (Fig. 1-H) .....3  
2' Pygofer with sides of posteromedial emargination evenly tapered; style apex with third point short, much less than half distance between first and second points (Figs. 7-C, J, M) .....4
- 3 Pygofer dorsal appendage bifid distally in dorsal view (Ross 1965: Fig. 33-B), falcate in lateral view; aedeagus with shaft apex in posterior view broadened and truncate with median notch (ibid: Fig. 33-A) .....*amicus* (Ross)  
3' Pygofer dorsal appendage simple, extended ventrad, then bent posterad (Fig. 4-K); aedeagus with shaft apex in posterior view entire, without notch (Fig. 7-F) .....*moyai*, n. sp.
- 4 Pygofer dorsal appendage broad basally, with spinelike distal projection(Fig. 4-M); aedeagus with apex in posterior view broadly rounded (Fig. 7-M) .....*pueblensis*, n. sp.  
4' Pygofer dorsal appendage evenly tapered from base to apex (Fig. 4-J); aedeagus with apex in posterior view truncate with pair of laterally directed spines (Fig. 7-B) .....*elliptica*, n. sp.

*Nelionidia elliptica*, new species

(Figs. 2-J; 4-J; 7-A–D; 11-Q)

**Type locality:** ca. La Huerta, Jalisco, Mexico.

**Diagnosis.** Length of male 2.7mm. Head pale yellow, anteclypeus and areas adjacent to clypeogenital suture brown, apex infused with orange, crown with pair of brown preapical spots well developed; pronotum margins pale, medial area with symmetrical brown markings; mesonotal triangles and mesothoracic venter dark brown; scutellum yellow infused with brown; forewing brown, with large white spots at base of clavus, base of corium, and subapically in brachial cell; costal brochosome field and veins yellow. Male abdominal 2S apodemes short, extended dorsomesad, not reaching posterior margin of sternite III. Pygofer (Fig. 4-J, 11-Q) with posteromedial emargination shallow, V-shaped; dorsal appendage extended ventrad, then abruptly bent posterad, distal section slightly arcuate. Aedeagus (Figs. 7-A–D) with apex in lateral view tapered, in posterior view truncate with pair of lateral projections; long paired processes arising preapically adjacent to gonopore, sinuate in lateral view, in posterior evenly curved ventrolaterad, then mesad, apices extended to near midline. Style apex (Fig. 7-A) with first and second points broad, third point short, acute, arising near midpoint between first and second points and angled toward first point.

**Material examined.** Holotype ♂, MEXICO: Jalisco, ca. La Huerta, 480m, 19°27'47"N 104°39'13"W, 16 Oct 2001, S. H. McKamey, et al., fogging 3-FG [INHS].

**Note.** The species name refers to the form of the aedeagus in posterior view.

*Nelionidia moyai*, new species

(Figs. 1-H; 3-K, Z; 4K; 7-E–G; 11-R)

**Type locality:** ca. La Huerta, Jalisco, Mexico.

**Diagnosis.** Length of male 2.7mm, female 2.5–2.7mm. Coloration as described for *N. elliptica*. Male abdominal 2S apodemes short, extended dorsomesad, not reaching posterior margin of sternite III. Pygofer (Figs. 4-K, 11-R) with posteromedial emargination extended to base of segment, basal half parallel-sided; dorsal appendage extended ventrad, then

abruptly bent posterad, distal section elongate, much longer than basal section, nearly straight in lateral view. Aedeagus (Figs. 7-D–F) with apex truncate in posterior view (but see Note below); paired processes relatively short, extended ventrolaterad in posterior view. Style (Fig. 1-H) apex with third point slender, elongate, nearly as long as distance between first and second points, arising approximately two-thirds distance between first and second point.

**Material examined.** Holotype ♂, MEXICO: Jalisco, ca. La Huerta, 480m, 19°27'47"N 104°39'13"W, 16 Oct 2001, S.H. McKamey, et al., fogging 3-FI [INHS]; 2 ♂♂ paratypes, same data, except fogging 3-FG [INHS]. Other material: 1 ♀, same data as paratypes.

**Note.** The three available male specimens all appear to have the tip of the aedeagus broken; thus the true shape of this structure remains unknown. This species is named in honor of Dr. Gustavo Moya-Raygoza, Universidad de Guadalajara, author of numerous studies on the ecology of leafhopper vectors, who facilitated the collection of this and many other undescribed species of Cicadellidae during the senior author's 2001 fieldwork in Mexico.

*Nelionidia pallescens*, new species

(Figs. 3-M; 4-L; 7-H–K)

**Type locality:** ca. La Huerta, Jalisco, Mexico.

**Diagnosis.** Length of male 2.7mm, female 2.5. Coloration pale yellow overall, apex of head infused with orange, paired brown spots on crown small. Male abdominal 2S apodemes short, extended dorsomesad, not reaching posterior margin of sternite III. Pygofer (Fig. 4-L) with posteromedial emargination shallow, V-shaped; dorsal appendage extended ventrad, then abruptly bent posterad, distal section nearly straight, approximately equal to basal section in length. Aedeagus (Figs. 7-H, I) with apex blunt in lateral view, obtusangulate in posterior view, lateral processes elongate, extended ventrolaterad, weakly arcuate. Style apex (Fig. 7-J) resembling that of *N. elliptica*, but distance between first and second points shorter.

**Material examined.** Holotype ♂, MEXICO: Jalisco, ca. La Huerta, 480m, 19°27'47"N

104°39'13"W, 16 Oct 2001, S.H.McKamey, et al., fogging 3-BY [INHS]; 1 ♂ and 2 ♀ paratypes, same data [INHS].

**Note.** The species name refers to the pale overall coloration.

### *Nelionidia pueblensis*, new species

(Figs. 3-L; 4-M; 7-L–O; 11-D, S)

**Type locality:** Nicolás Bravo, Puebla, Mexico.

**Diagnosis.** Length of male 3.2–3.3mm, female 3.2mm. Coloration as in *N. elliptica*, but darkly pigmented areas more extensive and pale areas smaller. Male abdominal 2S apodemes short, extended dorsomesad, not reaching posterior margin of sternite III (Fig. 11-D). Pygofer (Figs. 4-M, 11-S) with posteromedial emargination V-shaped, extended to near base of segment; dorsal appendage broad basally, gradually tapered distally, with slender spine arising on mesal surface preapically and extended ventromesad. Aedeagus (Figs. 7-L, M) with shaft relatively broad in lateral view; apex in lateral view bearing acute anteriorly directed spine, apex in posterior view flattened and broad with long paired processes extended ventrad and sinuately curved. Style apex (Fig. 7-O) footlike, third point reduced to obtuse projection.

**Material examined:** Holotype ♂, MEXICO: #05-239 Puebla, Nicolás Bravo, 2600m, N18.6198 W97.3058, 10 Nov 2005, R. Rakitov [INHS]; 3 ♂♂ paratypes, same data; 1 ♂ paratype, MEXICO: #05-230 Mexico, rt 190 10.8km W Rio Frio 3100m, N19.3195 W98.7436 9 Nov 2005, R. Rakitov [INHS].

**Note.** The species name refers to the state of Puebla, Mexico, in which the type series was collected.

### *Neoimbecilla*, new genus

(Figs. 2-K, L; 3-J, Y; 4-N, O; 7-P–U)

**Type species:** *Erythroneura kiperi* Beamer, here designated.

**Diagnosis.** Length 3.1–3.6mm. Coloration (Figs. 2-K, L) pale yellow overall with few brown spots or more extensive brown markings; crown unmarked; mesonotum brown anterolaterally; scutellum black; forewing with indistinct brown markings in basal half.

Head subequal to pronotum in width; crown angulately produced, slightly longer medially than next to eye; coronal suture incomplete. Forewing (Fig. 3-J) inner apical cell oblique, CuA subequal in length to CuP; third apical cell broadened distally; outer apical cell ca. 2X longer than wide. Hindwing vein RA obsolete; m-cu present or MP confluent with CuA for short distance. Pygofer (Figs. 4-N, O) broadly emarginate to base dorsally; without oblique dorsolateral internal ridge; with conspicuous microtrichia distally; with few or no fine setae; basolateral setal group well differentiated, setae short and stout; apical lobe with group of short slender setae on mesal surface; dorsal appendage well developed, short, broad, movably articulated to pygofer margin dorsally, anteroventral lobe connected by well-sclerotized tendon to dorsal apodeme of aedeagus; ventral appendage absent; unsclerotized areas restricted to margin. First segment of anal tube basal arm weakly sclerotized, extended to junction of aedeagal tendon and pygofer appendage; microtrichia inconspicuous. Subgenital plate (Figs. 4-N, O) with basolateral angle obtuse; dorsal fold indistinct; submarginal row with 3–4 macrosetae; marginal row with short slender setae, continuous from basolateral angle to apex; distal lobe weakly to strongly expanded. Connective (Figs. 7-R, U) V-shaped; stem short, bifid, compressed. Style (Figs. 7-Q, T) preapical lobe prominent; apophysis smooth, expanded distally with extremely elongate mesally curved third point. Aedeagus (Figs. 7-P, S) with or without preatrium; dorsal apodeme broadly expanded in lateral view; shaft simple, tubular; processes present or absent; gonopore terminal.

**Distribution.** Southwestern USA and Mexico.

**Notes.** The two included species were consistently paraphyletic with respect to the clade comprising *Illinigina* and *Hymetta* in the phylogenetic analysis, but constraining *Neoimbecilla* as monophyletic yielded trees only a single step longer. Despite the considerable differences between the two included species in coloration and pygofer structure, the short, stout, basolateral pygofer setae and the unique style apex seem sufficiently distinctive to warrant placing these species together in a genus distinct from other New World Erythroneurini. The genus name, which is feminine, was chosen to draw attention to the superficial similarity of the elongated style apex *Neoimbecilla* to those



found among species of the Afrotropical genus *Imbecilla* Dworakowska. The type species was previously placed in the “*ritana* group” of *Zygina* by Young (1952).

**Included species:**

*Neoimbecilla kiperi* (Beamer, 1929b:124) (*Erythroneura*), new combination  
*Neoimbecilla latiplata*, n. sp.

**Key to Males of *Neoimbecilla***

- 1 Pygofer dorsal appendage with two or three prominent spines distally (Fig. 4-N); subgenital plate not expanded distally; aedeagus with pair of short distal processes (Fig. 7-S) .....*kiperi* (Beamer)  
1' Pygofer dorsal appendage tapered with apex truncate (Fig. 4-O), without spines; subgenital plate strongly broadened distally; aedeagus without distal processes.....*latiplata*, n. sp.

*Neoimbecilla latiplata*, new species

**Type locality:** Iguala, Guerrero, Mexico.  
**Diagnosis.** Coloration (Fig. 2-L) pale yellow overall; pronotum with pair of dark brown lateral maculae, mesonotum brown; scutellum black; forewing clavus with symmetrical diffuse brown infuscation in basal two-thirds, inner and middle anteapical cell infuscate distally. Male pygofer (Fig. 4-O) with dorsal appendage short, broad, tapered distally to truncate apex, curved downward. Subgenital plate (Fig. 4-O) with basolateral angle weakly developed, distal lobe strongly expanded, compressed, truncate apically. Aedeagus (Fig. 7-P) with shaft short, tapered in lateral view, apex depressed, without processes. Style (Fig. 7-Q) with third point nearly as long as rest of style, apex nearly reaching midline.  
**Material examined.** Holotype ♂, MEXICO: Guerrero, Iguala, 25-X-1941, DeLong, Good, Caldwell, and Plummer [INHS].  
**Note.** The species name refers to the broad subgenital plate.

*Neozygina*, new genus

(Figs. 1-G; 2-M; 3-N, AA; 7-V–X; 11-C, P)

**Type species:** *Erythroneura ceanothana* Beamer, here designated.  
**Diagnosis.** Length 2.5–3.3mm. Coloration (Fig. 2-M) usually yellowish or reddish overall with brown infuscation, crown with pair of well-delimited preapical brown spots, ventral half of anteclypeus and lateral margins of clypeus

usually brown, forewing variably infused with fuscous but without distinct color pattern, mesonotal triangles usually dark brown. Head slightly wider than pronotum; crown short, anterior and posterior margins subparallel, coronal suture incomplete. Forewing (Fig. 3-N) inner apical cell base oblique, length of CuA subequal to that of CuP; third apical cell slender, parallel sided, outer apical cell approximately 2X longer than wide; anal vein poorly delimited. Hind wing (Fig. 3-AA) vein RA present; m-cu crossvein absent, CuA confluent with MP for short distance or touching at one point. Sternite IX with median longitudinal internal ridge anteriorly. Pygofer (Figs. 5-B, 11-P) broadly emarginate to near base, without dorsolateral oblique internal ridge; surface usually with conspicuous microtrichia, with few or no fine setae; basolateral setal group inconspicuous or absent; apical lobe usually with distinct group of short slender setae on mesal surface; one or more macrosetae present near base of dorsal appendage; dorsal appendage rigidly attached, highly variable in form, arising from sclerotized dorsal ridge; postero-ventral appendage present, usually elongate and curved dorsomesad; unsclerotized areas present distally along ventral margin and usually also between dorsal and ventral appendages. First segment of anal tube with basolateral arm well developed and strongly sclerotized, not closely associated with base of sclerotized ridge of pygofer; microtrichia conspicuous. Subgenital plate (Fig. 5-B) with basolateral angle acute; without conspicuous dorsal fold; with submarginal row of three macrosetae; marginal row

of microsetae irregular but continuous from subbasal angle to near apex, setae short and slender; distal lobe digitiform, not expanded. Connective Y- or U-shaped; stem short, bifid, usually with median keel dorsally. Style (Fig. 7-W) preapical lobe greatly enlarged, usually truncate; apophysis, smooth, broad and truncate apically. Aedeagus (Fig. 7-V) with preatrium absent or short; dorsal apodeme narrow, weakly compressed, dorsal end expanded laterad, T-shaped in posterior view (Fig. 1-G), connections to pygofer membranous; shaft elongate, with paired apical or basal processes, or both; gonopore terminal or subterminal on posterior surface.

**Distribution.** Southern USA to Chile and Argentina.

#### Included species:

*Neozygina abluta* (McAtee, 1924d:132) (*Erythroneura*), new combination  
*Neozygina apacha* (Baker, 1925b:537) (*Erythroneura*), new combination  
*Neozygina arida* (Beamer, 1937b:31) (*Erythroneura*), new combination  
*Neozygina balli* (Beamer, 1932i:125) (*Erythroneura*), new combination  
*Neozygina bimaculata* (Baker, 1903d:9) (*Typhlocyba*), new combination  
*Neozygina ceonothana* (Beamer, 1934c:287) (*Erythroneura*), new combination  
*Neozygina davisii* (Beamer, 1934d:96) (*Erythroneura*), new combination  
*Neozygina huachucana* (Beamer, 1934c:287) (*Erythroneura*), new combination  
*Neozygina penapacha* (Beamer, 1941a:18) (*Erythroneura*), new combination  
*Neozygina quadricornis* (Beamer, 1930b:431) (*Erythroneura*), new combination

#### *Rossmoneura*, new genus

(Figs. 2-N; 5-A; 7-Y, Z)

**Type species:** *Erythroneura tecta* McAtee, here designated

**Diagnosis.** Length 2.5–3.6 mm. Ground color pale yellow, dorsum heavily marked with dark brown, tinged with red; crown usually with pair of somewhat diffuse brown spots preapically (Fig. 2-M); face with anteclypeus and lateral margin of frontoclypeus near antennal pit dark brown; mesosternum and mesonotal triangles dark brown; forewing with large transcommisural pale area near base, another covering distal part of clavus and extended to base of inner apical cell. Head subequal to or narrower than pronotum, crown short, slightly longer mesad than next to eye. Wing venation as in *Erasmoneura*. Male genital capsule and genitalia as in *Erasmoneura* except as follows: pygofer (Fig. 5-A) without distinct microtrichia distally, dorsal appendage without distinct basal line of

**Notes.** The genus name, which is feminine, combines “*neo*,” signifying new, with “*Zygina*,” the name of the genus in which the included species were formerly placed, and is meant to signify that the genus is endemic to the New World. The monophyly of *Neozygina* is supported by the presence of one or more macrosetae just basad of the dorsal pygofer appendage, a feature unique among New World Erythroneurini, and the absence of a ventro-lateral setal group on the pygofer. All of the North American species previously assigned to the “*ceonothana* group” of *Zygina* (sensu lato) by Young (1952) belong to this genus. Many undescribed species of this genus occur in Mexico, Central and South America.

weakening; aedeagus with median posterior preapical spine (Figs. 7-Y, Z), without paired spines or processes.

**Notes.** Species of this genus were not included in the phylogenetic analysis presented in this paper. Subsequent analyses (not shown) that included the type species did not support the inclusion of this species in *Erasmoneura*. These analyses failed to resolve the position of *R. tecta* unambiguously, but in a majority of most parsimonious trees the species was placed close to *Nelionidia* based on the similar pygofer structure and the presence of paired spots on the crown. *Rossmoneura* differs from *Nelionidia* in the structure of the aedeagus, which has preatrium elongate and the shaft with paired distal processes short, the anterodorsal preapical process absent, and a posteroventral preapical spine present, as well as in having the pygofer appendage immovably fused to the margin.

The genus name, which is feminine, was formed by combining the surname of the late

Prof. Herbert H. Ross, the pioneering insect systematist and educator whose well-curated collections largely form the basis for this revision,

with the last three syllables of *Erasmoneura*, the genus-group taxon in which the three included species were most recently placed.

### Included species:

*Rossmoneura calva* (Beamer, 1946b:22) (*Erythroneura*), new combination

*Rossmoneura carbonata* (McAtee, 1920a:289) (*Erythroneura*), new combination

*Rossmoneura tecta* (McAtee, 1920a:288) (*Erythroneura*), new combination

### *Zyginama*, new genus

(Figs. 1-E; 2-O; 3-O; 7-AA–CC)

**Type species:** *Erythroneura ritana* Beamer, here designated.

**Diagnosis.** Length 2.5–3.5mm. Coloration (Fig. 2-O) pale yellow to brownish overall, crown often with pair of somewhat diffuse brown or reddish preapical spots, pronotum and forewing often with symmetrical reddish markings. Head slightly narrower than pronotum, anterior margin angulately produced, crown longer medially than next to eyes; coronal suture complete. Wing venation (Figs. 3-O, BB) as in *Neozygina*. Sternite IX with median longitudinal internal ridge anteriorly. Pygofer (Fig. 1-E) broadly emarginate to near base, without dorsolateral oblique ridges; with indistinct microtrichia distally; fine setae very sparse or absent; ventrolateral setal group well developed, usually consisting of several macrosetae; distal lobe with several short slender setae on mesal surface; without macrosetae near base of dorsal appendage; dorsal appendage simple, spinelike, rigidly attached, arising from sclerotized dorsal ridge; ventral appendage present usually, elongate and curved dorsomesad (very short and inconspicuous in some spp.); unsclerotized areas present distally along ventral margin and usually also between dorsal and ventral appendages. First segment of anal tube with

basolateral arm well developed and strongly sclerotized, not closely associated with base of sclerotized ridge of pygofer; distal ring with conspicuous microtrichia. Subgenital plate (Fig. 1-E) with basolateral angle acute; without conspicuous dorsal fold; with submarginal row of three macrosetae; marginal row of macrosetae irregular but more or less continuous from subbasal angle to near apex, setae short and slender; distal lobe expanded in lateral view. Connective (Fig. 7-CC) U- or V-shaped; stem short, bifid, usually with median keel dorsally. Style (Fig. 7-BB) preapical lobe greatly enlarged, usually truncate; apophysis smooth, broad and truncate apically. Aedeagus (Fig. 7-AA) with preatrium short; dorsal apodeme well developed, weakly compressed, expanded dorsally in lateral view, dorsal end expanded laterad, T-shaped in posterior view, connections to pygofer membranous; shaft highly variable interspecifically, often with paired apical and/or basal processes; gonopore terminal or subterminal on posterior surface.

**Distribution.** Southern USA to Peru.

**Note.** The name is feminine and is modified from that of the genus in which the included species were previously placed. Most of the species formerly assigned to the “*ritana* group” of *Zygina* (s.l.) by Young (1952) apparently belong in this genus. Numerous undescribed species of this genus occur in Mexico and in Central and South America.

### Included species:

*Zyginama agnata* (Knull & Auten 1938a:537) (*Erythroneura*), new combination

*Zyginama ales* (Beamer 1932I: 124) (*Erythroneura*), new combination

*Zyginama arizonica* (Knull & Auten 1938a:536) (*Erythroneura*), new combination

*Zyginama aucta* (McAtee 1920a:279) (*Erythroneura*), new combination

*Zyginama bilocularis* (Van Duzee 1924a:233) (*Erythroneura*), new combination

*Zyginama blanda* (Knull & Auten 1938a:538) (*Erythroneura*), new combination

*Zyginama canyonensis* (Beamer 1929b:120) (*Erythroneura*), new combination

*Zyginama casta* (Beamer 1929b:118) (*Erythroneura*), new combination

*Zyginama cimarroni* (Beamer 1929b:119) (*Erythroneura*), new combination

*Zyginama cornigera* (Beamer 1937b:31) (*Erythroneura*), new combination

*Zyginama dentata* (Gillette 1898a:765) (*Erythroneura*), new combination



*Zyginama erosa* (McAtee 1924c:36) (*Erythroneura*), new combination  
*Zyginama grandis* (Beamer 1929b:127) (*Erythroneura*), new combination  
*Zyginama inclita* (Beamer 1934a:44) (*Erythroneura*), new combination  
*Zyginama iguala* (Ross 1965:263) (*Erythroneura*), new combination  
*Zyginama inornata* (McAtee 1924d:132) (*Erythroneura*), new combination  
*Zyginama merita* (Beamer 1932f:127) (*Erythroneura*), new combination  
*Zyginama modula* (Knull & Auten 1938a:535) (*Erythroneura*), new combination  
*Zyginama munda* (Knull & Auten 1938a:534) (*Erythroneura*), new combination  
*Zyginama nicholi* (Beamer 1927a:30) (*Erythroneura*), new combination  
*Zyginama novella* (Knull & Auten 1938a:536) (*Erythroneura*), new combination  
*Zyginama nuda* (Knull & Auten 1938a:538) (*Erythroneura*), new combination  
*Zyginama obscura* (Beamer 1929b:117) (*Erythroneura*), new combination  
*Zyginama pallenta* (Beamer 1929b:117) (*Erythroneura*), new combination  
*Zyginama pinalensis* (Beamer 1929b:119) (*Erythroneura*), new combination  
*Zyginama ritana* (Beamer 1934c:286) (*Erythroneura*), new combination  
*Zyginama rubicunda* (Beamer 1929b:126) (*Erythroneura*), new combination  
*Zyginama sola* (Knull & Auten 1938a:534) (*Erythroneura*), new combination  
*Zyginama spectabilis* (Knull & Auten 1938a:533) (*Erythroneura*), new combination  
*Zyginama ternaria* (Van Duzee 1924a:235) (*Erythroneura*), new combination  
*Zyginama triceroprocta* (Beamer 1929b:118) (*Erythroneura*), new combination  
*Zyginama tricolor* (Beamer 1929b:124) (*Erythroneura*), new combination  
*Zyginama tripunctata* (Beamer 1929b:124) (*Erythroneura*), new combination  
*Zyginama unicolor* (Beamer 1929b:120) (*Erythroneura*), new combination  
*Zyginama utahna* (Beamer 1937b:32) (*Erythroneura*), new combination

### South American Genera

#### *Amazygina*, new genus

(Figs. 1-I; 3-P, CC; 5-C–F; 8-A–P; 11-E–H, T)

**Type species:** *A. decaspina*, n. sp., here designated.

**Diagnosis.** Length 2.9–3.3mm. Coloration pale yellow or white overall; crown without paired spots, with or without dark median anterior macula (as in Fig. 2-P). Head wider than pronotum; crown short with anterior and posterior margins subparallel, without paired spots, some species with dark median apical macula, coronal suture incomplete. Forewing (Fig. 3-P) relatively broad, inner apical cell base oblique, length of CuA subequal to that CuP; third apical cell broadened distally, outer apical cell approximately 2X longer than wide; anal vein relatively well delimited. Hindwing (Fig. 3-CC) vein RA present; m-cu crossvein absent, CuA confluent with MP for short distance. Sternite IX with distinct median internal ridge. Pygofer (Figs. 5-C–F, 11-T) broadly emarginate dorsally to or near base of segment, without dorsolateral oblique ridges; dorsal appendage rigidly attached, arising near apex from sclerotized dorsal ridge, usually with one or more teeth;

surface smooth, without distinct microtrichia, with a few long fine setae; basolateral setal group well developed with several large setae; dorsoapical lobe with distinct group of short slender setae mesad of appendage. First segment of anal tube (Fig. 11-T) with basolateral arms well developed and strongly sclerotized, articulated to base of sclerotized ridge of pygofer; microtrichia conspicuous. Subgenital plate with basolateral angle usually acute; dorsal fold moderately well developed; submarginal row with 3–4 macrosetae; marginal row of microsetae irregular, very sparse distally, setae short and slender; distal lobe somewhat compressed and broadened. Connective (Fig. 8-C, G) Y or U-shaped; stem, when present, short, bifid. Style (Fig. 8-D) preapical lobe prominent, broadly rounded; apophysis slightly curved, apex truncate with imbricate texture at least ventrally. Aedeagus (Figs. 8-A, E, I, M) highly variable interspecifically, dorsal apodeme well developed, expanded and T-shaped in posterior view, dorsal connections to pygofer membranous; with long paired processes arising near base; with or without unpaired dorsal process anterad of gonopore-bearing shaft; gonopore terminal or subterminal on posterior surface.

**Distribution.** Ecuador.

**Note.** The genus name, which is feminine, was formed by combining “Amazon” the region in which the genus occurs, with “*Zygina*”, the genus to which species run in Young’s (1952) key. This genus appears to be endemic to South America. No previously described North American species belong to this genus, nor are any of the undescribed North American species presently in hand assignable to *Amazygina*.

**Included species:**

- Amazygina chela*, n. sp.
- Amazygina compressa*, n. sp.
- Amazygina decaspina*, n. sp.
- Amazygina depressa*, n. sp.

**Key to Males of *Amazygina***

- 1 Pygofer with dorsal appendage reduced to short, toothed projection (Figs. 5-D, F) .....2
- 1’ Pygofer with dorsal appendage well developed, spinelike (Figs. 5-C, E) .....3
- 2 Aedeagus without unpaired dorsal process between gonopore-bearing shaft and base; shaft with two pairs of long processes arising from base and extended along shaft and pair of slender retrorse spines arising just basad of gonopore (Fig. 8-E, F) .....*compressa*, n. sp.
- 2’ Aedeagal with unpaired dorsal process between gonopore-bearing shaft and base; with two pairs of basal processes arising near base, anterior pair trifurcate; without retrorse spines just basad of gonopore (Fig. 8-M, N) .....*decaspina*, n. sp.
- 3 Aedeagus with large, depressed, dorsal process between base and gonopore-bearing shaft, gonopore-bearing shaft tubular, with pair of slender apical spines (Fig. 8-I, J) .....*depressa*, n. sp.
- 3’ Aedeagus in lateral view with a single short, tapered shaft bearing pair of slender elongate dorsally directed spines (Fig. 8-A, B) .....*chela*, n. sp.

***Amazygina chela*, new species**

(Figs. 5-C; 8-A–D; 11-E)

**Diagnosis.** Length of male 3mm. Male 2S apodemes short, narrow, extended dorsomesad (Fig. 11-E). Crown unmarked; anteromedial area and lateral triangles of mesonotum brown. Pygofer dorsal appendage C-shaped, with dorsal preapical tooth (Fig. 5-C). Aedeagus (Figs. 8-A, B) with short tapered gonopore-bearing shaft and pair of elongate slender processes arising near base of shaft and extended posterodorsad. Style apex footlike, second point long (Fig. 8-D).

**Material examined.** Holotype ♂, EC-UADOR: Orellana, Transect Ent. 1 km S Onkonegare Camp, Reserva Etnica Waorani,

The genus is described based on four new species, all of which were found in rainforest canopy-fogging samples from eastern Ecuador. Some specimens of all four species were collected in the same sample, suggesting that they were feeding on the same (unknown) host plant. Although the samples contained males and females, reliable morphological features separating females were not found. Males are separable using the following key.

00°39’10”S, 076°26’00”W; lot#1440, 7-Feb-96, T. L. Erwin, et al., fogging terra firme forest [USNM]; 2 ♂♂ paratypes, same data except lot#1406, 4-Feb-96 [USNM], and lot#1028, 12-Feb-99 [INHS].

**Note.** The species name refers to the claw-like pygofer appendage. The size of the dorsal preapical tooth of this appendage varies intra-specifically, with some specimens having the spine larger than shown in Fig. 5-C.

***Amazygina compressa*, new species**

(Figs. 2-P; 5-D; 8-D–F; 11-F)

**Diagnosis.** Length of male 3.3mm. Crown apex with diffuse median brown macula (Fig. 2-P); mesonotum brown anteromedially; lateral triangles brown. Male 2S apodemes short,

rounded, extended dorsomesad (Fig. 11-F). Pygofer dorsal appendage short, bidentate (Fig. 5-D). Aedeagal shaft (Figs. 8-E, F) not divided, tubular, apex compressed, obliquely truncate in lateral view; pair of slender retrorse spines just basad of gonopore on posterior preapical surface; paired basal processes somewhat flattened and twisted preapically, as long as shaft. Style (Fig. 8-H) with preapical lobe present but not prominent; apex with two points subequal in size.

**Material examined.** Holotype ♂, EC-UADOR: Orellana, Transect Ent. 1 km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W; lot#1440, 7-Feb-96, T. L. Erwin, et al., fogging terra firme forest [USNM]. Additional material: 1 ♀, same data as holotype [USNM].

**Note.** The species name refers to the compressed distal portion of the aedeagal shaft.

#### *Amazygina decaspina*, new species

(Figs. 1-I; 3-P, CC; 5-F; 8-M-P; 11-H)

**Diagnosis.** Length of male 3mm. Crown apex with diffuse median brown macula (as in Fig. 2-P); mesonotum brown anteromedially, lateral triangles brown; mesosternum brown. Male 2S apodemes robust, well separated at base, rounded, extended posteromesad, nearly reaching posterior margin of sternite III (Fig. 11-H). Pygofer dorsal appendage (Fig. 5-F) similar to that of *A. compressa*. Aedeagus (Figs. 8-M, N) with dorsal process between base and gonopore-bearing shaft compressed, acuminate in lateral view; gonopore-bearing shaft tubular with apex acuminate; two pairs of basal processes present; posterior pair slender and straight, extended dorsad and curved posterad apically; anterior pair divided near midlength into three processes, one extended anterad, one short slender pair extended dorsad, and a longer pair extended dorsad and strongly arched anterad beyond shaft apex. Style apex hatchet-like (Fig. 8-P).

**Material examined.** Holotype ♂, EC-UADOR: Orellana, Transect Ent. 1 km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W; lot#1560, 21-Jun-96, T. L. Erwin, et al., fogging terra firme forest [USNM]. Paratypes: 4 ♂♂, same data as holotype; 6 ♂♂, same data except lot#1440, 7-Feb-96 [USNM, INHS]; 1 ♂, ECUADOR:

Orellana, Tiputini Biodiversity Sta. nr Yasuni Nat. k 220-250m, 00°37'55"S, 076°08'39"W, 7-Feb-99, T. L. Erwin, et al., Lot#2040, Transect T/5, fogging terra firme forest [USNM]. Additional material: 2 ♀♀, same data as holotype; 2 ♀♀, same data except lot#1440, 7-Feb-96 [USNM, INHS].

**Note.** The species name refers to the aedeagus, which has a total of 10 spinelike processes, including the gonopore-bearing shaft.

#### *Amazygina depressa*, new species

(Figs. 5-E; 8-I-L; 11-G, T)

**Diagnosis.** Length of male 3mm. Male 2S apodemes subquadrate, not reaching posterior margin of sternite III (Fig. 11-G). Color uniformly pale yellow except forewing apex weakly infuscated. Pygofer dorsal appendage long and slender, strongly arcuate, with short preapical spine extended posterad (Fig. 5-E). Aedeagus (Figs. 8-I, J) with large strongly depressed anterior dorsally directed process; process in posterior view broad, tapered and acute apically; gonopore-bearing shaft short, slender, tubular; apex truncate, with pair of short, slender posterolateral spines; basal processes as long as anterior process. Style apex small, footlike (Fig. 8-L).

**Material examined.** Holotype ♂, EC-UADOR: Orellana, Transect Ent. 1 km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W; lot#1560, 20-June-96, T. L. Erwin, et al., fogging terra firme forest [USNM]; 1 ♂ paratype, same data [INHS]; 1 male paratype, same data except lot#1440, 7-Feb-96 [USNM]. Additional material: 3 ♀♀, same data as holotype; 1 ♀, same data as second male paratype [USNM, INHS].

**Note.** The species name refers to the large depressed dorsal process of the aedeagus.

#### *Hamagina*, new genus

(Figs. 2-P; 3-Q; 5-G-I; 9-A-L; 11-I-K, U)

**Type species:** *H. spinigera*, n. sp., here designated.

**Diagnosis.** Coloration (Fig. 2-P) pale yellow overall, dorsum heavily infuscated; crown with large median anterior brown macula; anterior half and lateral triangles of mesonotum, and mesosternum dark brown; forewing apex



infuscated. Wing structure and venation as in *Amazygina*. Sternite IX with median longitudinal internal ridge anteriorly. Pygofer (Figs. 5-G–I) shallowly emarginate dorsally (Fig. 11-U); without oblique anterolateral ridge; surface smooth, without conspicuous microtrichia or fine setae; basolateral setal group well differentiated, setae somewhat enlarged; distal lobe with well-developed preapical and apical group of short fine setae; dorsal margin without macrosetae; dorsal appendage well developed, short, falcate, rigidly attached to pygofer margin; ventral appendage present, slender, curved dorsomesad; lobe between appendages weakly sclerotized. First segment of anal tube (Fig. 11-U) with basolateral arm well developed, articulated near base of dorsal appendage; microtrichia conspicuous. Subgenital plate (Figs. 5-G–I) with basolateral angle prominent; dorsal fold weakly developed; submarginal row with three macrosetae; marginal row with short fine setae, more sparsely distributed distally; distal lobe not expanded, with or without prominent

dorsal spine. Connective (Figs. 9-B, E, H) Y- or U-shaped, stem short, bifid, overlapping aedeagal base. Style (Fig. 9-C) with preapical lobe prominent; apophysis smooth, apex attenuate or with two points. Aedeagus (Fig. 9-A) with preatrium short; dorsal apodeme crescent-shaped in lateral view, T-shaped in dorsal view, connections to pygofer membranous; with large median dorsal process between base and gonopore-bearing shaft; shaft with paired basal or preapical spines or processes; gonopore terminal.

**Distribution.** Ecuador and Peru.

**Notes.** The genus name, which is feminine, is derived in part from the Latin word “hamus” (hook) and refers to the large distal spine on the subgenital plate of two of the three known species. Phylogenetic analysis recovered the genus as sister to a clade comprising *Amazygina* and *Perugina*, n. gen. The genus is described based on three new species, two from lowland Amazonian rainforest and one from a cloud forest in the eastern Andean foothills.

Included species:

- Hamagina pascoensis*, n. sp.
- Hamagina serrata*, n. sp.
- Hamagina spinigera*, n. sp.

Key to Males of *Hamagina*

- 1 Subgenital plate with large distal spine (Figs. 5-H, I) .....2
- 1' Subgenital plate without distal spine (Fig. 5-G) .....*pascoensis*, n. sp.
- 2 Subgenital plate spine extended dorsad, gonopore-bearing shaft of aedeagus with numerous small lateral spines (Fig. 9-D) .....*serrata*, n. sp.
- 2' Subgenital plate spine extended mesad (Fig. 11-U), gonopore-bearing shaft of aedeagus without lateral spines (Fig. 9-G) .....*spinigera*, n. sp.

*Hamagina pascoensis*, new species

(Figs. 2-Q; 5-G; 9-A–C; 11-I)

**Diagnosis.** Length of male 3.7mm. Male 2S apodemes broad, triangular, extended nearly to posterior margin of sternite III (Fig. 11-I). Pygofer (Fig. 5-G) dorsal appendage with base perpendicular to sclerotized ridge, apex weakly arcuate, expanded and triangular in dorsal view; ventral appendage short, slender, curved posterodorsad along pygofer margin. Subgenital plate (Fig. 5-G) without distal spine.

Aedeagus (Fig. 9-A) with gonopore-bearing shaft with pair of small ventral preapical spines and pair of apical triangular teeth; pair of elongate slender processes arising near base and extended dorsad of shaft well beyond apex. Style apex (Fig. 9-C) footlike, heel (first point) prominent, toe (second point) elongate. **Material examined.** Holotype ♂, PERU: Pasco, Yanachaga-Chemillen N.P., 10°32'39.7"S, 75°22'0.1"W, 2300m, 10-13 Oct 2002, D. Takiya, C. Peña, R. Rakitov, Malaise trap acr. R. San Alberto [USML]. **Note.** The species name refers to the Peruvian department where the type specimen was collected.

***Hamagina serrata*, new species**

(Figs. 5-H; 9-D–F; 11-J)

**Diagnosis.** Length of male 3.2mm. Male 2S apodemes broad, triangular, extended nearly to posterior margin of sternite III (Fig. 11-J). Pygofer (Fig. 5-H) with dorsal appendage short, bifid distally, elevated above distal lobe; ventral appendage very short, slender, extended dorsad. Subgenital plate (Fig. 5-H) with prominent dorsally directed distal spine. Aedeagus (Fig. 9-D) with gonopore-bearing shaft tubular, with serrate flange posterolaterally and pair of posteroapical spines. Style apex (Fig. 9-F) with heel (point 1) poorly developed, section distad of heel elongate and sinuate.

**Material examined.** Holotype ♂, PERU: Madre de Dios, Rio Tambopata Res. 30 km (air) SW Pto. Maldonado, 290 m. 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, T. L. Erwin, et al. colls., 14 Sep 1984 01/02/46 [USNM].

**Note.** The species name refers to the serrate ventrolateral margin of the gonopore-bearing shaft of the aedeagus.

***Hamagina spinigera*, new species**

(Figs. 3-Q; 5-I; 9-G–I; 11-K, U)

**Diagnosis.** Length of male 2.8–3mm. Male 2S apodemes short, extended dorsomesad (Fig. 11-K). Pygofer (Fig. 5-I) with dorsal appendage broad, short, curved posteroventrad; ventral spine slender, curved dorsad. Subgenital plate with prominent preapical spine extended mesad (Figs. 5-I, 11-U). Aedeagus (Fig. 9-G) with gonopore-bearing shaft tridentate apically; pair of long, slender, nearly straight processes

extended posterodorsad between basal spine and gonopore bearing shaft. Style apex (Fig. 9I) flukelike, points subequal in size.

**Material examined.** Holotype ♂, EC-UADOR: Orellana, Transect Ent. 1 km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W; lot#1684, 1-Oct-1996, T. L. Erwin, et al., fogging terra firme forest [USNM]; 3 ♂♂ paratypes, same locality, lot#1573, 22-Jun-1996; lot#1084, 2-Jul-95; lot#1211, 6-Oct-95 [USNM, INHS].

**Note.** The species name refers to the well-developed distal spine on the subgenital plate.

***Napogina*, new genus**

(Figs. 2-R; 5-J, K; 10-A–H; 11-L)

**Type species:** *N. sinuata*, n. sp., here designated

**Diagnosis.** Length 2.8mm. Closely resembling *Amazygina* overall, but differing as follows: pygofer appendage simple, tapered, not elevated above dorsal margin, without teeth or basal process (Figs. 5-J, K); style apophysis (Figs. 10-C, H) attenuate, without distinct sculpturing, preapical heel small or absent; aedeagus (Figs. 10-A, B, E, F) with paired subapical processes, basal processes absent.

**Distribution.** Ecuador.

**Notes.** The name *Napogina*, which is feminine, is based on that of the Napo region of Ecuador where both included species occur. The phylogenetic analysis recovered the genus as a monophyletic sister to the clade comprising new genera *Hamagina* and *Spinigina*.

**Included species:***Napogina recta*, n. sp.*Napogina sinuata*, n. sp.**Key to Males of *Napogina***

- 1 Aedeagus (Fig. 10-E) with shaft arched posterad distally, with single pair of lamelliform processes, each bearing three fingerlike branches; style apex footlike (Fig. 10-H) .....*sinuata*, n. sp.
- 1' Aedeagus (Fig. 10-A) with shaft apex extended anterodorsad, with two pairs of simple, spinelike processes; style apex slender, acuminate (Fig. 10-C) .....*recta*, n. sp.

*Napogina recta*, new species

(Figs. 5-J; 10-A-C; 11-L)

**Diagnosis.** Length of male 2.8mm. Crown unmarked; anteromedian area and lateral triangles of mesonotum dark brown. Male 2S apodemes large, triangular, surpassing posterior margin of sternite III (Fig. 11-L). Pygofer with dorsal emargination extended nearly to base, broadly parabolic; dorsal appendage small, digitiform, arising near apex of dorsal margin but not extended to margin; apical margin truncate; ventrolateral setal group with 6–7 conspicuous setae. Subgenital plate (Fig. 5-J) with distal lobe broad, compressed, strongly bent dorsad. Connective (Fig. 10-D) compact, arms short and broad; stem bifid, strongly overlapping aedeagal preatrium. Style (Fig. 10-C) preapical lobe prominent, subangulate; apophysis slender, attenuate, evenly curved dorsolaterad. Aedeagus (Figs. 10-A, B) with preatrium short; dorsal apodeme tapered in lateral view, T-shaped in posterior view; shaft massive, long, recurved subrectangularly, with irregular serrate posterolateral flanges and two pairs of slender preapical processes, both extended anteroventrad, penultimate pair longer and curved more strongly anterad; gonopore apical.

**Material examined.** Holotype ♂, EC-UADOR: Orellana, Transect Ent. 1 km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W; lot#1494, 10-Feb-1996, T. L. Erwin, et al., fogging terra firme forest [USNM]; 1 ♂ paratype, same data except lot#959, 9-Feb-99 [USNM]. Additional material: 2 ♀♀, same data as paratype [USNM].

**Note.** The species name refers to the relatively straight distal section of the aedeagal shaft.

*Napogina sinuata*, new species

(Figs. 2-R; 5-K; 10-E-H)

**Diagnosis.** Length of male 2.8mm. Crown (Fig. 2-R) with indistinct pair of brown spots apically; anteromedial area and lateral triangles of mesonotum and mesosternum dark brown. Male 2S apodemes large, triangular, extended to posterior margin of sternite III. Pygofer (Fig. 5-K) with dorsal emargination extended to base, broad, nearly parallel-sided; dorsal appendage moderately large, falcate, curved ventromesad, not extended to apical margin;

apical margin truncate, with poorly sclerotized semicircular area ventrad of dorsal appendage; ventrolateral setal group with 4 conspicuous setae. Subgenital plate (Fig. 5-K) with distal lobe curved dorsad, compressed, somewhat expanded distally. Connective broadly U-shaped; stem bifid, strongly overlapping aedeagal preatrium. Style (Fig. 10-H) with preapical lobe well developed but small; apophysis elongate with footlike apex, heel bent laterad. Aedeagus (Figs. 10-E, F.) with preatrium short; dorsal apodeme slightly expanded dorsally in lateral view, T-shaped in posterior view; shaft depressed and straplike, in lateral view bent rectangularly, with distal portion arched posterad toward apex; two pairs of preapical lateral processes present, penultimate pair slender and spinelike, more distal pair longer, flattened and bifurcate, with ventral branch twisted and overlapping dorsal branch; gonopore apical; median distal spine present dorsad of gonopore.

**Material examined.** Holotype ♂, EC-UADOR: Orellana, Transect Ent. 1 km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W; lot#1406, 4-Feb-1996, T. L. Erwin, et al., fogging terra firme forest [USNM]; 2 ♂♂ paratypes, same data except lot#1579, 22-Jun-96 [USNM, INHS]. **Note.** The species name refers to the sinuate aedeagal shaft.

*Perugina*, new genus

(Figs. 3-R; 5-L; 10-I-L; 11-M)

**Type species:** *P. denticula*, n. sp., here designated.

**Diagnosis.** Length 2.8mm. Color pale yellow overall; crown with pair of indistinct brown spots preapically (as in Fig. 2-R); anteromedial area and lateral triangles of mesonotum and mesosternum dark brown. Head wider than pronotum; crown short with anterior and posterior margins subparallel, without distinct markings, coronal suture incomplete. Wing venation (Fig. 3-R) as in *Amazygina*. Sternite IX with distinct median and two lateral longitudinal internal ridges. Pygofer (Fig. 5-L) broadly emarginate to near base, with pair of short broad dorsolateral apodemes, without dorso-lateral oblique ridges; dorsal appendage rigidly attached, small, dentate, arising near apex from sclerotized dorsal ridge; surface smooth, without distinct microtrichia, numerous long



fine setae; basolateral setal group well developed with several large setae; dorsoapical lobe with distinct group of short slender setae mesad of appendage. First segment of anal tube with basolateral arm well developed, strongly sclerotized, articulated to base of sclerotized ridge of pygofer; microtrichia conspicuous. Subgenital plate (Fig. 5-L) with basolateral angle acute; with dorsal fold moderately well developed; submarginal row with three macrosetae; marginal row of microsetae irregular but continuous from subbasal angle to near apex, setae short and slender. Connective (Fig. 10-K) Y-shaped, stem short, bifid, overlapping aedeagal preatrium. Style (Fig. 10-L) preapical lobe prominent, broadly rounded; apophysis slightly curved, apex avicephaliform with imbricate texture. Aedeagus (Figs. 10-I, J) with preatrium short, articulated near fork of connective; dorsal apodeme long, narrow, compressed, dorsal connections to pygofer membranous; shaft elongate, tubular, with long paired basal processes, apex acuminate; gonopore terminal, surrounded by minute denticuli.

**Distribution.** Peru.

**Notes.** The genus name, which is feminine, is based on that of the country where specimens of the only known species were collected. Phylogenetic analysis placed *Perugina* as sister to *Amazygina*. This genus is readily identified by the structure of the pygofer, which lacks appendages and is conspicuously clothed with long, fine setae.

#### Included species:

*Perugina denticula*, n. sp.

#### *Perugina denticula*, new species

**Diagnosis.** Length of male 2.8mm. Coloration as described for genus. Male abdomen with 2S apodemes short, rounded, extended dorsomesad (11-M). Aedeagus (Figs. 10-I, J) with basal processes long, sinuate. Style apex (Fig. 10-L) subtruncate with small median tooth.

**Material examined.** Holotype ♂, PERU: Madre de Dios, Rio Tambopata Res. 30 km (air) SW Pto. Maldonado, 290 m. 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, T. L. Erwin, et al. colls., 06 Sep 1984 05/02/156 [USNM]; 3 ♂♂ paratypes, same data [USNM, INHS]; 1 ♂ paratype, same data except 07 May 1984, 05/02/072 [USNM].

#### *Spinigina*, new genus

(Figs. 3-S; 5-M, N; 10-M-T; 11-N)

**Type species:** *S. hirsuta*, n. sp., here designated.

**Diagnosis.** Length 3mm. Head wider than pronotum; crown short with anterior and posterior margins subparallel, with pair of somewhat diffuse brown spots preapically, coronal suture incomplete. Wing venation (Fig. 3-S) as in *Amazygina*. Sternite IX with distinct median longitudinal internal ridge. Pygofer (Figs. 5-M, N) broadly emarginate to near base, without dorsolateral oblique ridges; dorsal appendage rigidly attached, falcate, arising near apex from sclerotized dorsal ridge; surface smooth, without distinct microtrichia, with sparse fine setae; basolateral setal group well developed with several large setae; apical lobe with distinct group of short slender setae; ventral appendage short and inconspicuous or absent. First segment of anal tube with basolateral arm well developed and strongly sclerotized, articulated to base of sclerotized ridge of pygofer; pair of broad spinose ventolateral lobes distally. Subgenital plate (Figs. 5-M, M) with basolateral angle obtuse; without conspicuous dorsal fold; with submarginal row of three macrosetae; marginal row of microsetae irregular but continuous from subbasal angle to near apex, setae short and slender. Connective (Figs. 10-O, R) U- or V-shaped, stem short, bifid. Style (Figs. 10-P, Q) preapical lobe prominent, truncate; apophysis sickle-shaped, apex attenuate with small preapical tooth. Aedeagus (Figs. 10-M, N, S, T) with preatrium short, articulated near fork of connective; dorsal apodeme long, narrow, and weakly compressed, dorsal connections to pygofer membranous; shaft elongate, depressed, with long paired distal processes; gonopore preapical or terminal.

**Distribution.** Peru.

**Notes.** This genus is readily distinguished by the reduced or absent ventral pygofer appendage, the long slender style apophysis, and the presence of numerous short spines on the first segment of the anal tube, a feature unique among known Erythroneurini and upon which the genus name (feminine) is based. The genus is based on two new species from Rio Tambopata Reserve, Madre de Dios, Peru, described below.

**Included species:***Spinigina hirsuta*, n. sp.*Spinigina quadrispinosa*, n. sp.**Key to Males of *Spinigina***

- 1 Pygofer without ventral appendage (Fig. 5-N); aedeagus (Figs. 10-S, T) with two pairs of distal processes, apex depressed, broad in posterior view; style apex (Fig. 10-Q) evenly curved laterad, without distinct heel-like angle ..... *quadrispinosa*, n. sp.
- 1' Pygofer with small ventral appendage (Fig. 5M); aedeagus (Figs. 10-M, N) with one pair of distal processes, apex compressed, slender in posterior view; style apex (Fig. 10-P) abruptly bent laterad, with distinct heel-like angle ..... *hirsuta*, n. sp.

***Spinigina hirsuta*, new species**

(Figs. 3-S; 5-M; 10-M-P; 11-N)

**Diagnosis.** Length of male 3mm. Male 2S apodemes large, rounded, extended beyond posterior margin of sternite III (Fig. 11-N). Pygofer (Fig. 5-M) with dorsal appendage short, sinuate, arising subapically from sclerotized ridge. Aedeagus (Figs. 10-M, N) with shaft compressed, bearing two long, robust preapical lateral processes curved ventrolaterad; posteroventral angle of shaft adjacent to gonopore clothed with minute, hairlike spines. Style apex (Fig. 10-P) footlike with distinct heel.

**Material examined.** Holotype ♂, PERU: Madre de Dios, Rio Tambopata Res. 30 km (air) SW Pto. Maldonado, 290 m. 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, T. L. Erwin, et al. colls., 07 Nov 1983 01/02/48 [USNM]; 1 ♂ paratype, same data except 14 Sep 1984 01/02/73 [USNM].

**Note.** The species name refers to the presence of numerous small hairlike spines on the aedeagus.

***Spinigina quadrispinosa*, new species**

(Figs. 5-N; 10-Q-T)

**Diagnosis.** Length of male 3mm. Male 2S apodemes large, rounded, extended beyond posterior margin of sternite III. Pygofer (Fig. 5-N) with dorsal appendage extended to aedeagus (Figs. 10-M, O) with dorsal sub-basal hump; pair of slender preapical processes extended ventrad then bent anterad; second pair extended dorsad and curved anterolaterad; unpaired distal process arched over apex from

left to right. Style apex (Fig. 10-Q) sicklelike, apex without distinct heel.

**Material examined.** Holotype ♂, PERU: Madre de Dios, Rio Tambopata Res. 30 km (air) SW Pto. Maldonado, 290 m. 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, T. L. Erwin, et al. colls., 06 Sep 1984 05/02/156 [USNM].

**Note.** The species name refers to the four paired lateral spines of the aedeagal shaft.

**CONCLUDING REMARKS**

Although the New World fauna of Erythroneurini comprises more than 700 described species and many more await discovery and description, the fauna appears to be less phylogenetically diverse than that of the Old World. The color patterns exhibited by North American species are remarkably varied, but other aspects of the morphology, particularly the structure and chaetotaxy of the male genital capsule and the shape of the connective and styles, are more conservative in the New World fauna. In particular, the connective is U- or V-shaped in all known New World species, in contrast to the multitude of forms found among Old World species, a majority of which have a median anterior lobe between the two lateral arms. The subgenital plates in nearly all known New World species have an angulate basolateral projection (present in many but not all Old World genera) and a basal submarginal row of three macrosetae. The pygofer appendages are limited to a few basic forms, with most New World species having the dorsal appendage immovably fused to the pygofer side (in contrast to the Old World, in which the vast majority of species appear to have movably articulated dorsal appendages). *Erythroneura* and the taxa formerly included as

its subgenera have the style apex with a third point of various forms, but the more basal parts of the style are conservative in the New World fauna; and, with the exception of a few South American species, species of genera endemic to the Neotropical and western Nearctic regions nearly all have a simple, truncate style apex. The depauperate erythroneurine fauna of South America, evidenced by the lack of previously described species from that continent, appears to be confirmed by recent canopy fogging in Amazonia, as well as Malaise trap sampling in Andean premontane forests, and in the more arid grasslands and deserts of Chile and Argentina (unpublished data). Such samples contain an abundance of individuals and species of the typhlocybine tribes Dikraneurini, Empoascini, and Alebrini, but very few Erythroneurini. South American tropical and subtropical grasslands and savannas have not yet been sampled intensively for leafhoppers and these biomes may yet yield diverse erythroneurine taxa, as do similar habitats in Asia and Africa. In contrast, Mexico appears to harbor a rich, but largely undescribed erythroneurine fauna.



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## APPENDIX A

**Morphological Characters for Phylogenetic Analysis of Erythroneurini****Head**

1. Width: 0, narrower than pronotum; 1, as wide as or wider than pronotum.
2. Crown: 0, anterior margin strongly produced and angulate medially (Fig. 2-D); 1, anterior margin slightly produced, longer medially than next to eye (Fig. 2-M); 2, weakly produced, anterior and posterior margins parallel.
3. Coronal suture: 0, extended to crown apex; 1, incomplete, not reaching crown apex; 2, absent or very short ( $< 1/4$  distance to crown apex).
4. Ocelli: 0, well developed; 1, absent or vestigial.
5. Eye: 0, narrower than vertex width; 1, as wide as or wider than vertex width.
6. Face in profile: 0, not depressed,  $45^\circ$  or more from horizontal; 1, depressed, less than  $45^\circ$  from horizontal.
7. Male anteclypeus: 0, narrow, depressed, as in female; 1, inflated, broad, in contrast to that of female.
8. Maxillary plate: 0, not extended laterad of lorum; 1, expanded laterad of lorum, lorum well separated from lateral margin of face (Fig. 1-A).

**Thorax**

9. Pronotum: 0, without conspicuous pits; 1, with conspicuous pits.
10. Forewing vein CuA: 0, distinctly shorter than CuP (Fig. 1-B); 1, subequal to CuP (Fig. 3-D); 2, distinctly longer than CuP (Fig. 3-C).
11. Forewing vein CuA: 0, longer than MP; 1, shorter than MP (Fig. 1-B); 2, CuA absent (MP connected to Cu stem).
12. Forewing inner apical cell: 0, elongate, parallel-sided through most of its length (Fig. 1-B); 1, wide basally, tapered distally; 2, very short and oblique.
13. Inner (fourth) apical cell base: 0, oblique, apex of Cu and m-cu crossvein forming continuous line (Fig. 3-A); 1, distinctly angulate (Fig. 3-D); 2, transverse (Fig. 1-B).
14. Second apical cell base: 0, quadrate (Fig. 1-B); 1, petiolate.
15. Third apical cell: 0, widened distally (Fig. 3-P); 1, parallel sided (Fig. 1-B); 2, narrowed distally.
16. Third apical cell: 0, straight (Fig. 1-B); 1, curved (Fig. 3-Q).
17. Outer (first) apical cell: 0, short, length  $< 2$  times width (Fig. 3-M); 1, length subequal to 2 times width (Fig. 1-B); 2, elongate, length distinctly greater than 2 times width (Fig. 3-R).
18. Anal (claval) vein: 0, visible throughout length (Fig. 3-Q); 1, obsolete (Fig. 3-C).
19. Forewing appendix: 0, absent; 1, present.
20. Hindwing apex: 0, broadly rounded (Fig. 3-V); 1, distinctly narrowed (Fig. 3-T); 2, truncate (Fig. 3-U).
21. Hindwing submarginal vein: 0, complete (RA present along costal margin and continuous with submarginal vein at wing apex); 1, extended to apex of RP or RM; 2, absent at wing apex (Fig. 1-C).
22. Hindwing vein RA: 0, present (Fig. 1-C); 1, absent.
23. Hindwing vein RP: 0, free; 1, absent or fused to MA (Fig. 1-C).
24. Hindwing veins MP and CuA: 0, separate, connected by crossvein, or touching at one point (Fig. 3-W); 1, fused for short distance, then divergent (Fig. 1-C); 2, completely confluent.
25. Hindwing veins MP and CuA: 0, divergent distally (Fig. 1-V); 1, parallel (Fig. 1-C); 2, convergent distally (Fig. 1-U); 3, CuA reduced or absent distally.
26. Hindwing vannal vein (Pcu+A1): 0, branched (Pcu and A free distally); 1, unbranched (Pcu and A completely confluent; Fig. 1-C).
27. Front femur AM1 seta: 0, absent or undifferentiated (Fig. 1-D); 1, enlarged, on ventral margin.
28. Front femur AV: 0, setae subequal; 1, with two or more basal setae enlarged; 2, one basal seta distinctly larger than others (Fig. 1-D).
29. Front femur PV: 0, without fine basal setae; 1, with fine basal setae.
30. Middle femur: 0, with 2 dorsoapical macrosetae; 1, with 1 dorsoapical macroseta.
31. Hind tibia AV: 0, with 4 macrosetae; 1, with 5 macrosetae; 2, with 6 macrosetae; 3, with 7 or more macrosetae.

**Male abdomen**

32. 2S abdominal apodemes: 0, small, narrow, extended dorsomesad (Fig. 7-M); 1, large, broad, extended to or near 3S posterior margin (Fig. 9-K); 2, large, broad, extended beyond 3S posterior margin.
33. Pygofer length relative to subgenital plate: 0, shorter (Fig. 1-E); 1, subequal; 2, longer.
34. Pygofer dorsoapical lobe: 0, rounded (Fig. 4-B); 1, angulate (Fig. 4-I); 2, acutely produced.

35. Tergite IX emargination: 0, extended to base of segment (Fig. 7-N); 1, extended ca. halfway to base of segment (Fig. 7-P); 2, shallow, not extended halfway to base of segment.
36. Pygofer dorsal membrane: 0, without fine setae; 1, with conspicuous fine setae.
37. Pygofer dorsal macrosetae: 0, absent; 1, one or two present (Fig. 5-B); 2, several present.
38. Pygofer ventroapical membranous area: 0, absent or inconspicuous; 1, well developed (Fig. 4-C).
39. Pygofer oblique dorsolateral internal ridge: 0, absent; 1, present (Fig. 4-F).
40. Pygofer basolateral setae: 0, undifferentiated; 1, in distinct group, small (Fig. 4-A); 2, distinctly enlarged (Fig. 1-E); 4, long and fine.
41. Pygofer distal setae: 0, undifferentiated; 1, in distinct group.
42. Pygofer long fine setae: 0, absent; 1, present, sparse; 2, numerous, conspicuous.
43. Pygofer microtrichia: 0, absent or inconspicuous; 1, well developed, at least distally.
44. Pygofer dorsal appendage: 0, movably articulated, ventral angle of base free (Fig. 4-A); 1, with distinct basal suture, but not movably articulated; 2, fused, without suture (Fig. 1-E); 3, absent (Fig. 4-I).
45. Pygofer dorsal appendage shape: 0, simple (Fig. 1-E); 1, simple, with additional small process at base; 2, bifurcate far from base (Fig. 4-N); 3, bifurcate near base, branches parallel; 4, bifurcate near base, branches widely separated (Fig. 4-C).
46. Pygofer appendage: 0, without small basal internal process; 1, with small basal internal process.
47. Pygofer dorsal appendage length: 0, not reaching pygofer apex; 1, reaching pygofer apex; 2, extended beyond pygofer apex.
48. Pygofer appendage dorsal branch: 0, subequal to ventral branch in length; 1, shorter than ventral branch in length.
49. Pygofer dorsal appendage, dorsal view: 0, straight or very slightly curved; 1, distinctly sinuate.
50. Pygofer dorsal appendage, lateral view: 0, straight; 1, curved upward; 2, curved downward.
51. Pygofer ventral appendage: 0, present (Fig. 1-E); 1, absent.
52. Sternite IX median longitudinal internal ridge: 0, absent; 1, present.
53. Subgenital plate lateral margin: 0, rounded; 1, straight; 2, distinctly widened subbasally; 3, with angulate subbasal projection (Fig. 6-A); 4, with distinct process.
54. Subgenital plate proportions: 0, section basad of medial constriction subequal to or shorter than distal section; 1, basal section longer than distal section.
55. Subgenital plate lateral subdistal fold: 0, absent or indistinct; 1, distinct, angulate.
56. Subgenital plate basal macrosetae: 0, absent; 1, one; 2, two-four (Fig. 1-I); 3, five-seven; 4, nine or more.
57. Subgenital plate macrosetal row: 0, uniseriate, along margin; 1, oblique, extended posteromesad; 2, scattered.
58. Subgenital plate marginal subbasal setae: 0, absent or poorly differentiated; 1, distinct, peglike, forming continuous row (Fig. 6-A); 2, peglike setae restricted to basolateral angle; 3, group of macrosetae present; 4, long fine setae present.
59. Subgenital plate distal macrosetae: 0, absent; 1, present.

## Genitalia

60. Style preapical lobe: 0, absent or weak; 1, prominent (Fig. 1-H); 2, cheliform; 3, greatly enlarged (Fig. 6-S); 4, acuminate; 5, auriculate.
61. Style apex: 0, smooth; 1, serrate; 2, crenulate (Fig. 1-I).
62. Style apex: 0, slender (Fig. 10-B); 1, truncate and expanded (footlike) (Fig. 1-I); 2, with 3 points (Fig. 1-H).
63. Style second point: 0, present only as angle or small tooth; 1, well developed (Fig. 1-H); 2, longer than third point. This and the following two characters are applicable only to those having the style apex with three points.
64. Style third point (apical extension): 0, reduced to small tooth (Fig. 7-A); 1, subequal to other points; 2, larger than but shorter than half distance between other points; 3, longer than half distance between other two points (Fig. 1-H); 4, as long as or longer than distance between other two points; 5, extremely elongate, curved mesad (Fig. 6-Q).
65. Angle between first and third point: 0, unknown (third point very short); 1, ca. 90°; 2, <90°; 3, >90°.
66. Aedeagus/connective articulation: 0, at apex of connective stem; 1, near connective fork (stem overlapping base of aedeagus).
67. Aedeagus dorsal apodeme, lateral view: 0, absent; 1, present, not expanded in lateral view (Fig. 6-B); 2, broadly expanded in lateral view (Fig. 1-F).



68. Aedeagus dorsal apodeme, posterior view: 0, very short or long and parallel-sided, connections to pygofer membranous; 1, with U- or V-shaped dorsolateral ligaments connected to anal tube and/or pygofer appendage (Fig. 6-H); 2, triangular or T-shaped, without distinct connection to anal tube or pygofer appendage (Fig. 1-G).
69. Aedeagus preatrium: 0, short; 1, elongate (Fig. 1-F).
70. Aedeagal shaft in posterior view: 0, symmetrical; 1, asymmetrical.
71. Aedeagal shaft, crosssection: 0, round; 1, depressed; 2, compressed.
72. Aedeagal shaft in lateral view: 0, slender; 1, broad.
73. Aedeagus apex in posterior view: 0, broadened; 1, slender, truncate; 2, acuminate.
74. Aedeagal shaft: 0, smooth; 1, denticulate distally.
75. Aedeagus dorsal process between phallobase and gonopore-bearing shaft: 0, absent; 1, present (Fig. 9-A).
76. Aedeagus preapical processes: 0, present basally, well separated from shaft, longer than shaft; 1, present basally, well separated from shaft, shorter than shaft; 2, present basally, close to shaft, about as long as shaft; 3, present basally, close to shaft, much shorter than shaft; 4, two pairs of processes present; 5, arising near midlength of shaft; 6, arising near apex of shaft; 7, with unpaired ventral process.
77. Ventral processes, relative position: 0, evenly divergent; 1, divergent at base, then parallel; 2, slightly divergent, appressed to sides of aedeagal shaft; 3, parallel to each other on ventral side of shaft; 4, divergent only at apex; 5, one pair parallel to shaft, other strongly divergent; 6, unpaired.
78. Aedeagus paired distal processes: 0, long, apical (Fig. 1-G); 1, short, apical; 2, long, subapical; 3, short, subapical; 4, absent.
79. Apical processes, shape: 0, slender (Fig. 1-G); 1, small, toothlike; 2, flattened, triangular (Fig. 6-K).
80. Aedeagus dorsal distal lobe: 0, absent; 1, small; 2, large (Fig. 1-D).
81. Connective, median anterior lobe: 0, absent (Fig. 1-I); 1, present, broad; 2, present, slender.
82. Connective arms: 0, short; 1, long.
83. Connective stem: 0, absent or very short; 1, well developed, entire; 2, bifid.
84. Connective stem: 0, depressed; 1, compressed.
85. Anal tube processes: 0, absent (partially sclerotized aedeagal ligaments may be present); 1, present only as sclerotized rodlike basolateral arms (Fig. 4-I); 2, separate processes arising from basal apodemes
86. Anal tube vestiture: 0, without lateral spines (microtrichia may be present); 1, with numerous lateroapical spines (Fig. 5-N).

### Coloration

87. Ground color of dorsum: 0, pale yellow or white; 1, dark reddish or brown.
88. Vertex: 0, unicolorous or with indistinct markings; 1, with pair of dark preapical spots (Fig. 2-I); 2, with large median apical spot (Fig. 2-P); 3, with orange parallel submedial lines (often with lateral branch) (Fig. 2-C); 4, with oblique lateral vittae (Fig. 2-A); 5, with median triangular area extended onto thorax; 6, mostly dark with small pale lines or spots (Fig. 2-D).
89. Vertex midline: 0, pale; 1, dark.
90. Face: 0, without black spots anterodorsad of antennal pits; 1, with black spots anterodorsad of antennal pits (Fig. 1-A).
91. Anteclypeus: 0, concolorous with rest of face; 1, brown or black, contrasting with pale face (Fig. 1-A).
92. Pronotum: 0, without Y- or V-shaped medial vitta; 1, with Y- or V-shaped medial vitta (Fig. 2-B).
93. Mesonotum: 0, without dark lateral triangles; 1, with dark lateral triangles (Fig. 2-F).
94. Scutellum apex: 0, concolorous with rest of scutellum; 1, dark, contrasting with adjacent pale areas (Fig. 2-K).
95. Forewing: 0, without numerous irregular red dots; 1, with numerous irregular red dots (Fig. 2-E).
96. Forewing: 0, without oblique vittae; 1, with vittae forming zigzag pattern (Fig. 3-B); 2, with broken, oblique vittae (Fig. 3-C).
97. Clavus: 0, unicolorous; 1, with separate basal and distal vittae; 2, with continuous vitta parallel to suture; 2, largely or entirely bright red.
98. Costal margin: 0, without dark spot; 1, with dark spot
99. Second apical cell: 0, without brown apical spot; 1, with brown apical spot.
100. Inner (fourth) apical cell: 0, without brown spot basally; 1, with brown spot basally (Fig. 3-B).

## APPENDIX B

## Taxa Examined for Phylogenetic Analysis

All taxa are deposited in INHS unless otherwise indicated.

**Outgroups.** *Dikraneura arizona* DeLong and Caldwell; *Empoasca* sp. C (Jalisco, Mexico); *Empoascini*, N. Gen. A. (Onkonegare, Orellana, Ecuador) [USNM]; *Empoascini*, N. Gen. B (Ivmaka Res. Sta., Papua New Guinea); *Eupteryx artemisiae* (Kirschbaum); *Jorumidia* sp. (Onkonegare, Orellana, Ecuador) [USNM]; *Joruma* sp. (Onkonegare, Orellana, Ecuador) [USNM]; *Kunzeana* sp. (La Reforma, Oaxaca, Mexico); *Linnavuoriana roseipennis* (Oshanin); *Paralebra* sp. (ca. Zenzontla, Jalisco, Mexico).

**Ingroup Old World Taxa.** *Asianidia pallescens* (Dlabola); *Arboridia apicalis* (Nawa); *Arboridia kermanshah* Dlabola; *Arboridia parvula* (Boheman); *Arboridia velata* (Ribaut); *Arboridia* sp. A (Japan); *Arboridia* sp. B (Lien Hua Chih, Taiwan); *Arboridia* sp. C (Meifeng, Taiwan); *Arboridia* sp. D (Tunshih, Taiwan); *Cerneura* sp. (Pakhuis Pass, South Africa); *Chujophila* sp. (Madagascar); *Coloana arcuata* Dworakowska; *Diomma pulchra* (Matsumura); *Diomma (Bunyipia)* sp. (Papua New Guinea); *Frutioidia* sp. (Madagascar); *Helionidia dlabolai* Dworakowska; N. Gen. A. (Papua New Guinea); N. Gen. B. (Islamabad, Pakistan); *Gambialoa asiatica* Dworakowska; *Gambialoa gambiensis* (Ross); *Mitjaevia amseli* (Dlabola); *Molopopterus* sp. (Madagascar); *Musbrnoia* sp. (N. Sumatra, Indonesia); *Ratburella* sp. (Taiwan); *Salka nigricans* (Matsumura); *Seriana ochrata* Dworakowska; *Tautoneura* sp. (N. Sumatra, Indonesia); *Tautoneura mori* (Matsumura); *Thaia subrufa* (Motschulsky); *Ziczacella heptapotamica* (Kuznetsova); *Zygina flammigera* (Geoffroy); *Zyginidia scutellaris* (Herrich-Schaeffer);

**Ingroup New World Taxa.** *Amazygina compressa*, n. sp.; *Amazygina depressa*, n. sp.; *Amazygina decaspina*, n. sp.; *Aztegina punctinota*, n. sp.; *Erasmoneura nigerrima* (McAtee); *Erasmoneura vulnerata* (Fitch); *Eratoneura bifida* (Beamer); *Eratoneura impar* (Beamer); *Eratoneura ligata* (McAtee); *Eratoneura maculata* (Gillette); *Eratoneura osborni* (DeLong); *Erythridula aesculella* (Ross and DeLong); *Erythridula aspera* (Beamer and Griffith); *Erythridula atrimucronata* Beamer; *Erythridula crevcoeuri* (Gillette); *Erythridula obliqua* (Say); *Erythroneura calycula* McAtee; *Erythroneura comes* (Say); *Erythroneura corni* Robinson; *Erythroneura kanwakae* Robinson; *Hamagina pascoensis*, n. sp.; *Hamagina spinigera*, n. sp.; *Hepzygina aprica* (McAtee); *Hepzygina milleri* (Beamer); *Hymetta balteata* McAtee; *Hymetta trifasciata* (Say); *Illinigena illinoiensis* (Gillette); *Mexigena oculata* (McAtee); *Napogina recta*, n. sp.; *Napogina sinuata*, n. sp.; *Nelionidia amicus* (Ross); *Nelionidia elliptica*, n. sp.; *Neoimbecilla kiperi* (Beamer); *Neoimbecilla latiplata*, n. sp.; *Neozygina ceonothana* (Beamer); *Neozygina quadricornis* (Beamer); *Perugina denticula*, n. sp.; *Spinigena hirsuta*, n. sp.; *Spinigena quadrispinosa*, n. sp.; *Zyginama canyonensis* (Beamer); *Zyginama iguala* (Ross); *Zyginama ritana* (Beamer)

### Data Matrix for Phylogenetic Analysis of Erythroneurini

[illegible]



Taxon	Character	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100		
Asiandia	1	1	3	0	0	2	0	1	0	1	0	1	0	1	?	?	?	1	1	1	0	0	0	?	?	0	8	7	7	0	0	0	0	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0			
Cemeura	1	1	2	0	0	2	0	1	0	1	0	4	0	1	?	?	?	1	1	1	2	1	0	0	0	0	8	7	7	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0		
Diompha	1	0	2	0	0	2	0	0	0	1	0	0	0	1	?	?	?	0	2	1	1	0	0	2	0	0	8	7	7	4	?	?	0	1	1	1	0	1	0	1	?	0	1	0	1	0	0	1	1	0	0		
Bunpia	1	1	2	0	0	2	0	0	0	1	0	0	0	1	?	?	?	0	2	1	1	0	0	2	0	0	8	7	7	4	?	?	0	1	1	1	0	1	0	1	?	0	1	0	0	1	1	0	0	0			
Gambusia	0	1	0	1	0	0	2	0	0	1	0	1	0	1	?	?	?	0	2	2	0	0	0	2	0	0	8	3	7	4	?	?	2	2	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0			
Gambusia gamb	0	1	3	0	0	2	1	2	1	1	0	1	0	1	?	?	?	0	2	2	1	0	0	2	0	0	8	7	7	4	?	?	2	2	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0			
Mitipevia	1	1	3	0	1	2	2	2	0	1	0	1	?	?	?	?	?	1	1	1	0	2	1	1	2	0	2	2	4	?	?	1	2	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0			
Nemobioia	1	1	0	1	0	3	2	1	0	0	0	0	?	?	?	?	?	0	2	1	1	0	0	0	0	0	1	2	4	?	?	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
N.Gen.B	1	0	2	0	1	2	0	0	0	0	2	0	0	?	?	?	?	0	2	1	1	0	0	2	0	0	8	7	7	4	?	?	0	1	1	1	0	0	0	?	?	0	0	1	0	0	0	1	1	0	0		
Salka nigr	0	0	3	0	0	1	2	1	1	0	1	0	1	?	?	?	?	1	1	0	0	0	0	1	0	0	8	7	7	1	0	0	0	0	1	2	0	0	0	1	2	1	0	?	0	0	0	0	0	0			
Tauiou sp	0	1	3	0	0	2	1	1	1	0	1	0	1	?	?	?	?	1	2	1	1	0	0	2	0	0	8	7	7	0	0	0	0	2	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0			
Tauiou mori	1	1	3	0	0	2	0	1	0	1	0	1	?	?	?	?	?	1	2	1	0	1	0	0	0	0	8	7	7	0	0	0	0	2	1	1	1	2	0	0	0	4	0	0	0	0	0	2	1	1	1		
Thaia subr	1	0	0	1	1	2	0	4	0	2	0	0	?	?	?	?	?	1	0	1	0	0	0	0	0	0	3	2	4	?	?	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0			
Ziczagella	1	0	3	0	0	2	1	1	0	1	0	2	1	3	2	1	0	1	0	1	0	0	0	2	0	0	0	1	1	2	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0				
Zygania	1	1	2	0	0	2	2	1	1	0	0	1	?	?	?	?	?	0	2	0	1	0	0	0	0	0	8	7	7	4	?	?	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0			
Zygnidia	1	0	3	0	0	1	2	0	1	0	1	1	?	?	?	?	1	1	2	0	0	0	2	1	0	0	4	5	4	?	?	0	2	1	0	1	1	2	0	0	0	1	1	0	1	0	0	0	0				
Chuphiolia	0	0	3	0	0	2	0	2	0	3	0	1	?	?	?	?	?	0	2	2	1	0	0	0	0	0	8	7	7	0	0	0	0	1	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0			
Frutuloidea	1	0	3	0	0	2	0	2	0	1	0	1	?	?	?	?	1	1	1	0	0	0	0	0	0	0	8	7	7	0	0	0	0	2	0	1	1	0	1	2	0	0	1	0	?	0	0	0	0	0			
Helionidia	1	1	3	0	1	2	0	2	0	1	0	1	?	?	?	?	?	0	2	1	0	0	0	0	0	0	8	7	7	0	0	0	0	1	2	0	1	1	0	?	?	1	0	1	0	0	0	0	0	0			
Molopopterux	1	1	3	0	1	2	0	2	0	1	0	1	?	?	?	?	?	0	2	1	0	0	0	0	0	0	8	7	7	0	0	0	0	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0			
Hymettal bal	1	0	3	0	1	2	0	1	0	3	0	1	?	?	?	?	?	1	2	1	1	0	0	0	0	0	2	2	1	0	0	0	0	1	0	1	2	1	0	0	0	0	0	0	0	0	1	1	5	0	?		
Hymettai tri	1	0	3	0	1	2	0	1	0	3	0	1	?	?	?	?	?	1	2	1	1	0	0	0	0	0	1	0	2	4	?	?	0	0	1	2	1	0	0	0	0	0	0	0	0	0	1	1	5	0	?		
Arboud parv	1	0	2	0	1	2	0	1	0	1	0	2	1	2	1	1	1	1	2	1	1	0	0	2	0	0	1	0	0	0	?	?	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0			
Arboud vela	1	0	2	0	1	2	0	1	0	1	0	2	1	2	1	1	1	1	2	1	0	0	0	2	1	0	0	3	2	1	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Arboud apic	1	1	3	0	0	2	0	1	0	1	0	2	2	2	1	1	1	1	2	1	0	0	0	0	0	0	0	7	7	4	?	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Arboud spA	1	1	3	0	0	2	0	1	0	1	0	1	?	?	?	?	?	1	2	1	0	0	0	2	0	0	8	7	7	3	0	0	0	2	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0			
Arboud spB	1	0	3	0	0	2	0	1	0	1	0	1	?	?	?	?	?	1	2	1	0	0	0	2	0	0	8	7	7	0	0	0	0	2	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0			
Arboud spC	1	0	3	0	0	2	0	1	0	1	0	1	?	?	?	?	?	1	2	1	0	0	0	2	0	0	8	7	7	4	?	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Arboud spD	1	0	2	0	1	2	2	1	0	5	0	1	?	?	?	?	?	1	2	1	0	0	0	0	0	0	2	3	4	?	?	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Arboud kerm	1	0	3	0	1	2	0	1	0	1	0	1	?	?	?	?	?	1	2	1	0	0	0	0	0	0	8	7	7	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Erythri aesc	1	1	3	0	1	2	0	1	0	1	0	2	1	2	1	1	1	1	2	1	1	0	0	2	0	0	0	8	7	7	4	?	?	2	0	1	0	0	0	0	0	4	0	0	?	?	?	0	5	0	0		
Erythri crev	1	1	3	0	1	2	0	1	0	1	0	2	1	2	1	1	1	1	0	0	0	0	0	0	0	0	8	7	7	1	2	0	0	1	0	0	0	0	0	0	4	0	0	?	?	?	0	0	3	0	0		
Erythri obli	1	0	3	0	1	2	0	1	0	1	0	2	1	3	1	1	1	1	0	0	0	0	0	0	0	0	3	3	4	?	?	0	0	1	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0			
Erythri aspe	1	1	3	0	1	2	0	1	0	1	0	2	2	?	?	?	?	1	2	1	1	0	0	0	0	0	8	7	7	4	?	?	0	0	1	0	0	0	0	0	0	4	0	0	?	?	?	0	0	2	0	0	
Erythri atr	1	1	3	0	1	2	0	1	0	1	0	2	2	1	2	1	1	1	0	0	0	0	0	0	0	0	8	7	7	4	?	?	0	0	1	0	0	0	0	0	0	5	1	0	?	?	?	?	0	0	3	0	0
Erasmus nige	1	0	3	0	1	2	0	1	0	1	0	2	0	4	1	1	1	1	0	0	0	0	0	0	0	0	8	7	7	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0			
Erasmus vult	1	0	3	0	1	2	0	1	0	1	0	2	0	2	1	1	1	1	0	0	0	0	0	0	0	0	8	7	7	0	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0			
Erythri caly	1	0	3	0	0	2	0	1	0	1	0	2	1	1	1	1	1	2	2	1	0	0	0	0	0	0	0	4	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Erythro come	1	1	3	0	0	2	0	1	0	1	0	2	1	4	2	2	2	?	?	?	?	?	?	?	?	0	0	4	1	2	0	0	0	0	0	0																	

**APPENDIX D Apomorphies for terminal taxa and internal nodes of cladogram (Fig. 12) based on ACCTran (accelerated transformation) optimization. Non-homoplastic changes are indicated by \*.**

Node	Apomorphies
87	2(2), 20(1), 44(3), 91(0), 93(0)
88	13(2), 35(2), 39(0), 69(1), 81(1)
89	15(1), 17(2), 41(0), 43(1), 73(1), 91(1)
90	2(2), 40(3), 83(2)
91	3(2), 28(2), 33(1), 44(0), 51(0), 71(2), 77(3), 78(4), 84(0)
92	13(1), 32(0), 40(0), 50(1), 58(2), 66(0), 82(0)
93	35(1), 49(1), 51(0), 73(1), 79(1), 88(2), 89(1)
94	78(0), 88(2)
95	25(2), 77(1), 80(2), 84(0)
96	2(2), 45(1), 58(1), 61(2), 77(0), 78(4)
97	32(0), 75(1), 76(2), 78(1)
98	3(0), 6(1), 53(2), 84(0)
99	18(0)
100	25(2), 49(1), 71(1), 80(2), 86(1)*
101	10(1), 16(1), 20(1), 39(0), 67(1), 78(2), 81(0), 83(2)
102	2(1), 24(0), 28(0), 44(2), 58(0), 68(2), 85(1), 93(1)
103	13(0), 20(0), 42(1), 43(0), 69(0), 71(0)
104	10(0), 39(1), 52(1), 66(1), 82(1), 85(2)
105	2(0), 13(1), 53(3), 78(0), 81(2), 84(1)
106	18(1), 40(2), 71(2)
107	13(1), 25(3), 28(1), 39(1), 42(1), 79(1), 91(1)
108	2(2), 16(1), 32(1), 34(2), 50(1), 53(0), 54(1), 76(1)
109	6(1), 11(1), 15(1), 21(0)*, 30(0)*, 35(1), 71(2), 72(1), 77(3), 79(2), 83(0)
110	23(0), 31(0), 37(0), 43(0), 57(0), 72(1), 73(0), 78(1)
111	5(1), 10(2), 13(1), 41(0), 54(0)
112	14(0), 37(2), 71(2), 73(2), 89(1), 93(1)
113	3(0), 25(3), 31(1), 35(1), 44(2), 53(1), 61(1), 79(2), 83(2), 85(2)
114	5(0), 10(0), 19(0)*, 23(1)*, 29(0)*, 31(0), 33(0), 37(0), 40(0), 41(1), 58(0), 68(1), 87(0), 88(0), 92(0)
115	12(2), 20(0), 42(2), 53(3), 62(1), 68(2), 81(2)
116	4(1), 12(0), 21(2)*, 51(1), 56(0), 59(0), 69(0), 77(2), 84(1)
117	8(1), 14(0), 22(0), 24(1), 26(1), 44(0), 54(0), 56(2), 67(2), 82(1)
118	13(0), 27(0)*, 28(0), 57(0), 58(1)
119	17(1), 60(1), 85(0)
120	10(2), 62(1), 81(1), 82(0), 84(0)
121	25(1), 28(2), 35(0), 69(1), 73(2)
122	2(0), 25(2), 42(2), 43(0), 44(1), 58(4)
123	1(0), 10(1), 32(0), 68(0)
124	38(1), 66(1), 84(1), 93(1)
125	68(1), 81(0), 82(1), 88(1), 91(1), 94(1)
126	67(1), 71(2), 72(1), 76(2), 81(2)
127	53(3), 55(1), 84(0)
128	3(0), 20(0), 39(1), 53(2), 79(2), 88(1)
129	24(0), 32(2), 63(0), 64(1), 77(1)
130	10(2), 32(1), 49(2), 62(2), 71(2), 76(3), 79(1), 83(0)
131	17(0), 78(1), 88(2), 89(1)
132	10(0), 15(1), 83(2), 94(0)

133	20(0), 25(2), 39(1), 65(2)
135	40(1), 49(0), 52(0), 64(0), 77(1), 78(2), 91(1)
134	15(0), 20(1), 25(1), 35(1), 84(1)
136	10(0), 13(1), 20(2), 25(2), 43(0), 45(1), 60(3), 69(1), 74(1), 77(2), 83(2), 95(1)*, 97(5)
137	44(1), 48(0), 49(0), 50(1), 62(1), 72(1), 73(0), 76(0), 79(1)
138	39(1), 69(0), 97(0)
139	15(0), 25(1), 42(1), 64(5), 84(1), 94(1)
140	10(2), 50(1), 63(0), 78(0), 83(2), 87(1), 88(6)
141	48(1), 99(1)
142	47(1), 55(1), 71(2), 91(1), 98(0)
143	45(4), 46(0), 50(1), 68(2), 78(1), 83(0), 96(1), 100 (0)
144	13(2), 64(1), 73(0), 74(0), 76(0)
145	24(0), 71(2)
146	10(0), 11(1), 88(3), 98(1)
147	17(2), 24(1), 65(2), 74(1), 79(2)
148	44(2), 46(1), 48(2), 55(0), 64(3), 92(1), 96(2), 97(1), 100 (1)
149	13(1), 20(2), 44(1), 49(1), 83(1)
150	39(0), 40(1), 52(0), 77(4), 88(0)
151	18(0), 71(2), 73(2), 76(0), 80(2)
152	97(2)
153	18(1), 65(1), 69(1), 73(1)
154	89(0)
155	55(1), 88(4), 93(0)
156	2(0), 6(1), 10(1), 24(0)
157	49(2), 62(2), 73(0), 83(0), 89(1), 97(3)
158	52(1), 55(0), 69(0), 77(0), 91(0)
159	32(1), 48(2), 50(0), 78(0)
160	35(2), 42(0), 51(1), 76(7), 94(1)
161	49(0), 72(0), 80(2)
162	3(2), 28(0), 66(0), 88(0)
163	18(1), 32(2), 67(2), 76(3), 78(4), 89(0), 91(0), 93(0)
164	32(0), 40(2), 42(1), 48(0), 67(0), 71(2), 72(1), 77(2), 78(2), 97(1)
165	45(5)
166	76(3), 84(1), 94(1)
167	2(1), 24(0), 28(0), 37(1), 66(0)
168	10(2), 49(2), 51(0), 85(1), 91(1)
169	2(0), 3(0), 6(1), 10(1), 39(0), 60(3), 68(2), 89(1)
170	25(1), 35(1), 38(0), 44(2), 67(1)
Amazyg comp	10(0), 66(0), 78(2), 83(0)
Amazyg depr	41(0), 48(0), 71(1), 93(0)
Amazyg deca	32(1), 72(1)
Asianidia	11(1), 16(1), 22(1), 32(0), 83(1), 85(2), 88(0)
Arborid apic	15(0), 63(2), 76(7)
Arborid kerm	16(1), 18(1), 76(3)
Arborid parv	17(1), 76(1), 77(0), 78(0)
Arborid vela	45(2), 49(0), 64(4), 69(0), 72(1), 73(0)
Arborid spA	1(1), 15(0), 45(2), 71(2), 78(3), 80(2)
Arborid spB	1(1), 10(0), 13(1), 17(1), 73(0), 88(0), 91(0), 97(2)
Arborid spC	18(1), 62(1), 77(4), 78(4), 94(1)
Arborid spD	14(1), 15(2), 22(1), 49(2), 50(0), 54(1), 57(2), 60(5), 78(1), 90(1)
Aztegina	44(1), 50(1), 52(0), 73(0), 78(1), 83(0), 88(2), 94(1)
Bunyipia	7(1), 42(2), 52(1), 69(1), 73(0), 76(7), 78(1), 90(1), 94(1), 98(1)
Cerneura	11(2), 15(2), 53(2), 58(1), 60(4), 67(1), 84(0), 89(1)
Chujophila	1(0), 7(1), 16(1), 22(1), 38(1), 51(0), 52(0), 60(3), 76(7), 85(2)



Coloana	2(2), 3(0), 28(0), 40(3), 44(2), 49(2), 53(3), 67(1), 69(0), 80(2), 85(1)
Dikraneura	2(0), 3(0), 8(0), 24(0), 26(0), 37(2), 41(0), 50(0), 51(0), 53(1), 55(1), 56(4), 57(1), 59(1), 60(2), 68(0), 78(1)
Diomma	1(0), 3(0), 6(1), 10(1), 18(1), 44(1), 55(1), 58(0), 71(2), 87(1), 96(1), 97(1)
Empoasca spC	16(1), 28(1), 39(1), 42(1), 67(0), 68(0), 72(1)
EmpoasciniA	2(0), 3(2), 7(1), 14(1), 16(1), 17(1), 58(4), 89(0)
EmpoasciniB	2(2), 11(1), 12(0), 15(1), 33(1), 34(2), 40(3), 53(0), 57(1), 58(3), 83(1), 84(1), 88(2), 91(1)
Erasmon nige	15(0), 17(0), 64(4), 80(1)
Erasmon vuln	24(1), 45(2), 65(2), 99(1)
Eraton bifid	45(2), 47(1), 64(4), 92(0), 96(0)
Eraton impar	35(1), 45(3), 50(0), 63(0), 64(0), 72(1)
Eraton ligat	2(1), 17(1), 47(1), 52(1), 55(1), 96(1)
Eraton macul	52(1), 71(1), 78(1), 89(1)
Eraton osbor	15(0), 49(0), 63(0), 69(0), 76(3), 77(1)
Erythri aesc	17(2), 97(5)
Erythri aspe	63(2), 74(1)
Erythri atri	71(2), 88(5)
Erythri crev	32(1), 43(0), 71(1), 78(1), 79(2)
Erythri obli	14(1), 52(0), 64(3), 76(3), 77(3)
Erythro caly	17(1), 38(0), 65(1), 88(1), 96(0), 97(2)
Erythro come	11(2), 52(1), 64(4), 100 (1)
Erythro corn	11(2), 18(0), 24(0), 34(1), 73(2), 74(1), 76(8), 78(4), 80(2), 87(1), 88(6), 89(1)
Erythro kanw	17(1), 32(1)
Eupteryx	23(0), 31(1), 35(0), 40(1), 51(0), 56(1), 71(2), 78(0)
Frutioidea	12(1), 32(1), 40(0), 58(2), 67(1), 71(1), 73(0), 87(1), 88(2), 91(1), 99(1)
Gambial asia	34(2), 76(3), 80(2)
Gambial gamb	33(0), 35(1), 49(1), 50(2), 57(1), 59(1), 69(1)
Hamag pasc	32(1), 35(2)
Hamag spin	16(0)
Helionidia	3(0), 6(1), 10(2), 18(0), 32(2), 47(1), 49(1), 55(1), 68(1), 76(3), 80(1), 88(1)
Hepzig apri	22(1), 25(2), 83(0)
Hepzyg mill	10(1), 45(1), 49(1), 50(1)
Hymetta bal	10(2), 78(1)
Hymetta tri	3(2)
Illinigina	22(1), 24(1), 52(1), 76(2), 98(1), 100 (1)
Joruma	32(0), 33(1), 56(2), 59(0), 69(0), 83(1)
Jorumidia	35(2), 53(0), 60(1), 68(0), 71(0), 76(3), 87(1)
Kunzeana	10(1), 13(1), 44(2), 67(1), 76(5)
Linnavuoriana	6(1), 18(1), 88(1), 93(1)
Mexigina	3(1), 10(1), 20(1), 35(0), 44(3), 47(1), 55(1), 58(2), 79(2), 84(1), 90(1), 97(3)
Mitjaevia	28(1), 38(0), 41(0), 43(0), 52(1), 57(2), 58(2), 80(1), 82(0), 84(1), 87(1)
Molopopterus	4(0), 11(1), 18(0), 32(1), 33(1), 34(2), 55(1), 68(1), 69(0), 80(2)
Musbrnoia	1(0), 9(1)*, 25(1), 28(1), 38(1), 43(0), 52(1), 56(3), 57(2), 73(0), 81(1)
N.Gen.B	17(0), 20(0), 22(1), 55(1), 58(0), 60(2), 62(0), 92(1), 96(1), 97(1), 98(1)
N.Gen.A	7(1), 15(1), 40(1), 43(0), 44(1), 60(3), 78(0), 94(1)
Napog recta	50(0), 62(0), 73(1), 82(0)
Napog sinua	32(1), 49(2), 79(2)
Nelion amic	45(3), 55(1), 64(4), 71(2), 72(1), 83(2), 87(1), 90(1)
Nelion elli	2(1), 13(1), 35(2), 41(0), 50(1), 51(0), 58(0), 63(2), 89(0)
Neoimb kipe	28(1), 45(2), 55(0), 78(3), 80(1)
Neoimb lati	52(1)
Neozyg ceon	49(1), 50(2), 52(0), 69(1), 71(1), 82(0)
Neozyg quad	45(4), 71(2), 72(1), 77(4), 80(2)

Neozyg spA	17(2), 34(1), 80(2)
Neozyg spB	61(2), 67(2), 69(1), 73(0), 78(1)
Perugina	16(0), 34(2), 44(3), 52(0), 55(1), 62(2), 68(0), 74(1), 75(0), 76(0), 83(0)
Ratburella	17(0), 32(1), 39(1), 40(1), 47(1), 49(1), 50(1), 57(1), 58(3), 78(0)
Salka nigr	13(1), 35(2), 37(1), 38(0), 40(1), 42(1), 43(0), 50(1), 51(0), 57(1), 67(1), 68(0), 69(0), 73(1), 87(1)
Seriana	10(1), 16(1), 42(0), 49(2), 52(0), 68(0), 80(1), 81(0), 88(2)
Spinig hirs	6(1), 35(1), 51(0), 71(2), 82(0), 83(0)
Spinig quad	60(3), 68(0), 78(0), 85(0), 88(1), 89(1)
Tauton mori	1(0), 17(0), 70(1)*, 88(4), 96(2), 97(1), 98(1), 99(1), 100 (1)
Tauton sp	11(1), 15(1), 22(1), 25(0), 51(0), 57(1)
Thaia subr	3(0), 22(1), 32(3), 35(1), 41(0), 44(2), 55(1), 58(4), 60(2), 66(1), 67(0), 76(3), 85(2)
Ziczacella	3(0), 18(1), 22(1), 39(0), 42(1), 43(0), 57(1), 64(3), 67(0), 69(1), 73(2), 76(0), 94(1), 96(1)
Zygina	6(1), 15(1), 18(1), 24(0), 35(1), 36(1)*, 41(0), 50(0), 52(1), 57(2), 59(1), 60(0), 71(2), 72(1), 92(1), 96(1), 97(1)
Zyginam cany	2(1), 3(1), 25(2), 33(1), 34(2), 88(1), 91(1), 96(2)
Zyginam igua	15(0), 43(0), 47(1), 50(2), 60(1), 67(1), 78(2), 99(1)
Zyginam rita	9(1), 52(0), 69(1), 73(1), 82(0)
Zyginidia	1(1), 3(0), 11(1), 22(1), 25(2), 32(1), 39(1), 40(1), 45(2), 68(2), 69(0), 76(4), 77(5), 85(2), 89(1)

## APPENDIX E      Old World Species Previously Placed in the Genus *Erythroneura*

### Species Placed in Other Genera

*Accacidia acaciae* (Linnavuori, 1962a: 72) (*Erythroneura*)  
*Accacidia dactyla* (Naudé, 1926a: 102) (*Erythroneura*)  
*Accacidia garhiensis* (Ahmed, 1970b: 181) (*Erythroneura*)  
*Accacidia improvisa* (Linnavuori, 1953d: 61) (*Erythroneura*)  
*Arboridia (Arboridia) adanae* (Dlabola, 1957a: 66) (*Erythroneura*)  
*Arboridia (Arboridia) agrillacea* (Anufriev, 1969b: 182) (*Erythroneura*)  
*Arboridia (Arboridia) alpestris* (Ribaut, 1959b: 400) (*Erythroneura*)  
*Arboridia (Arboridia) brevis* (Ribaut, 1931c: 407) (*Erythroneura*)  
*Arboridia (Arboridia) defecta* (Dlabola, 1957b: 294) (*Erythroneura*)  
*Arboridia (Arboridia) erecta* (Ribaut, 1931c: 402) (*Erythroneura*)  
*Arboridia (Arboridia) ithaburensis* (Linnavuori, 1962a: 70) (*Erythroneura*)  
*Arboridia (Arboridia) kermanshah* (Dlabola, 1963a: 310) (*Erythroneura*)  
*Arboridia (Arboridia) kratochvili* (Lang, 1945c: 96) (*Erythroneura*)  
*Arboridia (Arboridia) loginovae* (Emeljanov, 1964f: 19) (*Erythroneura*)  
*Arboridia (Arboridia) maculifrons* (Vilbaste, 1968a: 107) (*Erythroneura*)  
*Arboridia (Arboridia) pusilla* (Ribaut, 1936b: 74) (*Erythroneura*)  
*Arboridia (Arboridia) remmi* (Vilbaste, 1968a: 103) (*Erythroneura*)  
*Arboridia (Arboridia) ribauti* (Ossiannilsson, 1937a: 25) (*Erythroneura*)  
*Arboridia (Arboridia) silvarum* (Vilbaste, 1968a: 104) (*Erythroneura*)  
*Arboridia (Arboridia) simillima* (Wagner, 1939a: 201) (*Erythroneura*)  
*Arboridia (Arboridia) sputinkaensis* (Vilbaste, 1968a: 109) (*Erythroneura*)  
*Arboridia (Arboridia) velata* (Ribaut, 1952a: 451) (*Erythroneura*)  
*Arboridia (Arboridia) vitisuga* (Dlabola, 1963a: 312) (*Erythroneura*)  
*Arboridia (Arborifera) samadi* (Samad & Ahmed, 1979b: 2) (*Erythroneura*)  
*Arboridia (Arborifera) vinealis* (Ahmed, 1970a: 32) (*Erythroneura*)  
*Asianidia albula* (Lindberg, 1961a: 73) (*Erythroneura*)  
*Asianidia allagopappi* (Lindberg, 1954a: 248) (*Erythroneura*)  
*Asianidia alticola* (Lindberg, 1954a: 264) (*Erythroneura*)  
*Asianidia apiculata* (Horváth, 1909a: 295) (*Erythroneura*)  
*Asianidia asiatica* (Kusnezov, 1932a: 156) (*Erythroneura*)  
*Asianidia atlantica* (China, 1938c: 49) (*Erythroneura*)  
*Asianidia bystropogonis* (Lindberg, 1954a: 249) (*Erythroneura*)  
*Asianidia canariensis* (Metcalf, 1955a: 267) (*Erythroneura*)  
*Asianidia chinai* (Lindberg, 1961a: 71) (*Erythroneura*)  
*Asianidia chrysanthemi* (Lindberg, 1954a: 250) (*Erythroneura*)  
*Asianidia decolor* (Lindberg, 1936a: 15) (*Erythroneura*)  
*Asianidia insulana* (Lindberg, 1961a: 70) (*Erythroneura*)  
*Asianidia lactea* Lindberg 1954a: 250) (*Erythroneura*)  
*Asianidia madeirensis* (China, 1938c: 48) (*Erythroneura*)  
*Asianidia octofasciata* (Lindberg, 1936a: 11) (*Erythroneura*)  
*Asianidia perspicillata* (Horváth, 1909a: 295) (*Erythroneura*)  
*Asianidia rubropunctata* (Lindberg, 1936a: 14) (*Erythroneura*)  
*Asianidia salviae* (Lindberg, 1954a: 253) (*Erythroneura*)  
*Asianidia spartocytisi* (Lindberg, 1936a: 13) (*Erythroneura*)  
*Asianidia sublactea* (Lindberg, 1954a: 249) (*Erythroneura*)  
*Asianidia tejedae* (Lindberg, 1954a: 252) (*Erythroneura*)  
*Asianidia tenerifae* (Lindberg, 1936a: 13) (*Erythroneura*)  
*Asianidia vallicola* (Lindberg, 1954a: 251) (*Erythroneura*)  
*Beamerana tropicalis* (Osborn, 1928a: 288) (*Erythroneura*)  
*Cassianeura cassiae* (Ahmed, 1970a: 34) (*Erythroneura*)  
*Ciudadrea colorata* (Lindberg, 1936a: 12) (*Erythroneura*)  
*Ciudadrea magnifica* (Lindberg, 1954a: 243) (*Erythroneura*)  
*Dikraneura (Dikraneura) mali* (Provancher, 1890a: 297) (*Erythroneura*)  
*Empoasca carneola* (Osborn, 1928a: 288) (*Erythroneura*)  
*Empoascanara (Empoascanara) alami* (Ahmed, 1970b: 183) (*Erythroneura*)



*Empoascanara (Empoascanara) hazarensis* (Ahmed, 1970b: 179) (*Erythroneura*)  
*Empoascanara (Empoascanara) sathyamangalamensis* (Sohi & Kapoor, 1974a: 42) (*Erythroneura*)  
*Empoascanara (Empoascanara) truncata* (Ahmed, 1971b: 183) (*Erythroneura*)  
*Frutiodia (Dworakowskellina) amacula* (Linnavuori, 1965a: 16) (*Erythroneura*)  
*Frutiodia (Frutiodia) ricei* (Ross, 1965a: 265) (*Erythroneura*)  
*Gambialoa gambiensis* (Ross, 1965a: 265) (*Erythroneura*)  
*Hauptidia (Hauptidia) armata* (Ribaut, 1948a: 4) (*Erythroneura*)  
*Hauptidia (Hauptidia) provincialis* (Ribaut, 1931c: 414) (*Erythroneura*)  
*Hauptidia (Hauptidia) rivularis* (Linnavuori, 1962a: 72) (*Erythroneura*)  
*Hauptidia (Hauptidia) soosi* (Dlabola, 1952b: 31) (*Erythroneura*)  
*Hauptidia (Hauptidia) stellata* (Ribaut, 1948a: 5) (*Erythroneura*)  
*Helionidia cicadulosa* (Naudé, 1926a: 101) (*Erythroneura*)  
*Helionidia longifalx* (Linnavuori, 1953d: 62) (*Erythroneura*)  
*Helionidia quadrimaculata* (Naudé, 1926a: 100) (*Erythroneura*)  
*Henribautia hubbardi* (McAtee, 1924c: 35) (*Erythroneura*)  
*Imbecilla imbecilla* (Linnavuori, 1962a: 72) (*Erythroneura*)  
*Imbecilla lubiae* (China, 1931a: 53) (*Erythroneura*)  
*Kapsa mingorensis* (Ahmed, 1970a: 40) (*Erythroneura*)  
*Kropka unipunctata* (Dlabola, 1957c: 119) (*Erythroneura*)  
*Kusala salicis* (Ahmed, 1970a: 39) (*Erythroneura*)  
*Kusala setosa* (Ahmed, 1971b: 181) (*Erythroneura*)  
*Lamtoana flavoscuta* (Naudé, 1926a: 102) (*Erythroneura*)  
*Lectotypella kabiri* (Ahmed, 1971b: 179) (*Erythroneura*)  
*Lublinia gediensis* (Linnavuori, 1962a: 72) (*Erythroneura*)  
*Melicharidia aridula* (Linnavuori, 1956b: 138) (*Erythroneura*)  
*Mitjaevia amseli* (Dlabola, 1961b: 297) (*Erythroneura*)  
*Mitjaevia aurantiaca* (Mitjaev, 1969b: 1045) (*Erythroneura*)  
*Mitjaevia bibichanae* (Dlabola, 1961b: 296) (*Erythroneura*)  
*Molopopterus pulchra* (Naudé, 1926a: 103) (*Erythroneura*)  
*Molopopterus steeleae* (Ross, 1965a: 66) (*Erythroneura*)  
*Ossiannilssonola australis* (Walsh, 1862a: 149) (*Erythroneura*)  
*Protalebra sublunata* (Osborn, 1928a: 289) (*Erythroneura*)  
*Punctigerella betulae* (Vilbaste, 1968a: 112) (*Erythroneura*)  
*Punctigerella juchani* (Anufriev, 1971e: 520) (*Erythroneura*)  
*Punctigerella koreana* (Anufriev, 1971e: 521) (*Erythroneura*)  
*Punctigerella lamellaris* (Vilbaste, 1968a: 111) (*Erythroneura*)  
*Qadria cajanae* (Ahmed, 1971b: 185) (*Erythroneura*)  
*Rhusia maculicosta* (Naudé, 1926a: 99) (*Erythroneura*)  
*Sempia capreola* (Linnavuori, 1964a: 340) (*Erythroneura*)  
*Singapora cyclops* (Kusnezov, 1932a: 155) (*Erythroneura*)  
*Tamaricella atriplicis* (Lindberg, 1954a: 256) (*Erythroneura*)  
*Tamaricella cypria* (Ribaut, 1948a: 6) (*Erythroneura*)  
*Tamaricella franckeniae* (Lindberg, 1954a: 254) (*Erythroneura*)  
*Tamaricella fuerteventurae* (Lindberg, 1954a: 255) (*Erythroneura*)  
*Tamaricella tangigharuha* (Dlabola, 1957b: 295) (*Erythroneura*)  
*Tautoneura albida* (Dworakowska, 1970d: 353) (*Erythroneura*)  
*Tautoneura deska* (Dworakowska, 1970d: 348) (*Erythroneura*)  
*Tautoneura formosa* (Dworakowska, 1970d: 353) (*Erythroneura*)  
*Tautoneura fusca* (Dworakowska, 1970d: 353) (*Erythroneura*)  
*Tautoneura indefinita* (Dworakowska, 1970d: 348) (*Erythroneura*)  
*Tautoneura japonica* (Dworakowska, 1972g: 865) (*Erythroneura*)  
*Tautoneura leucothoe* (Kirkaldy, 1907d: 70) (*Erythroneura*)  
*Tautoneura marthae* (Linnavuori, 1960a: 268) (*Erythroneura*)  
*Tautoneura sinica* (Dworakowska, 1970d: 348) (*Erythroneura*)  
*Ziczacella dworakowskiae* (Anufriev, 1969c: 698) (*Erythroneura*)  
*Ziczacella heptapotamica* (Kusnezov, 1928b: 316) (*Erythroneura*)  
*Ziczacella lyriflora* (Dlabola, 1968a: 368) (*Erythroneura*)  
*Ziczacella steggerdai* (Ross, 1965a: 267) (*Erythroneura*)  
*Zygina (Hypericiella) digitata* (Ribaut, 1948a: 3) (*Erythroneura*)

*Zygina (Hypericiella) nebulosa* (Ribaut, 1948a: 3) (*Erythroneura*)  
*Zygina (Zygina) alnicola* (Linnavuori, 1965a: 35) (*Erythroneura*)  
*Zygina (Zygina) dorycnii* (Ribaut, 1936b: 52) (*Erythroneura*)  
*Zygina (Zygina) karatasa* (Dlabola, 1957a: 66) (*Erythroneura*)  
*Zygina (Zygina) ordinaria* (Ribaut, 1936b: 47) (*Erythroneura*)  
*Zygina (Zygina) rosincola* (Cerutti, 1939a: 84) (*Erythroneura*)  
*Zygina (Zygina) schneideri* (Günthart, 1974a: 24) (*Erythroneura*)  
*Zygina (Zygina) ulmi* (Ahmed, 1970a: 33) (*Erythroneura*)  
*Zygina (Zygina) ulmicola* (Mitjaev, 1971a: 118) (*Erythroneura*)  
*Zyginidia (Zyginidia) alexandrina* (Linnavuori, 1964a: 340) (*Erythroneura*)  
*Zyginidia (Zyginidia) alpicola* (Cerutti, 1939a: 86) (*Erythroneura*)  
*Zyginidia (Zyginidia) franzi* (Wagner, 1944b: 38) (*Erythroneura*)  
*Zyginidia (Zyginidia) lineata* (Lindberg, 1954a: 244) (*Erythroneura*)  
*Zyginidia (Zyginidia) mocsaryi* (Horváth, 1910b: 176) (*Erythroneura*)  
*Zyginidia (Zyginidia) younasi* (Ahmed & Samad, 1980) (*Erythroneura*)  
*Zyginopsis verticalis* (Ahmed, 1970a: 31) (*Erythroneura*)

### Species Incertae Sedis

*Erythroneura ariadne* Linnavuori, 1960b: 22  
*Erythroneura atropictila* Ahmed, 1970a: 35  
*Erythroneura cassavae* China, 1930a: 267  
*Erythroneura chaudhrii* Samad & Ahmed, 1979b: 2  
*Erythroneura claripennis* Naudé, 1926a: 98  
*Erythroneura doris* Kirkaldy, 1907d: 69  
*Erythroneura evansi* Ross, 1965a: 267  
*Erythroneura fulvidorsum* Naudé, 1926a: 98  
*Erythroneura harmsi* Izzard, 1936a: 600  
*Erythroneura honiala* Kirkaldy, 1906c: 365  
*Erythroneura honiloo* Kirkaldy, 1906c: 365  
*Erythroneura ipoloo* Kirkaldy, 1906c: 365  
*Erythroneura kashmirensis* Ahmed, 1970a: 37  
*Erythroneura lalage* Kirkaldy, 1907d: 70  
*Erythroneura leveri* Evans, 1948a: 131  
*Erythroneura lubra* Kirkaldy, 1906c: 364  
*Erythroneura macarangae* Linnavuori, 1960a: 266  
*Erythroneura melanogaster* Kirkaldy, 1906a: 364  
*Erythroneura modesta* Ahmed, 1970a: 41  
*Erythroneura nayavua* Linnavuori, 1960b: 21  
*Erythroneura plagiata* Heller & Linnavuori, 1968a: 17  
*Erythroneura postica* Heller & Linnavuori, 1968a: 17  
*Erythroneura rewana* Kirkaldy, 1907d: 71  
*Erythroneura sativae* Evans, 1940c: 12  
*Erythroneura shirozui* Ishihara, 1965  
*Erythroneura sidnica* Kirkaldy, 1907d: 69  
*Erythroneura sohii* Ahmed, 1985c: 251  
*Erythroneura subfumata* Heller & Linnavuori, 1968a: 16  
*Erythroneura toetoe* Cumber, 1952a: 525  
*Erythroneura urakensis* Samad & Ahmed, 1979b: 3  
*Erythroneura zealandica* Myers, 1923a: 424

### Nomina Nuda

*Erythroneura bistrig* Esaki & Ito, 1954a: 213  
*Erythroneura flavogutta* Esaki & Ito, 1954a: 215  
*Erythroneura hirtipennis* Lindberg, 1948b: 162

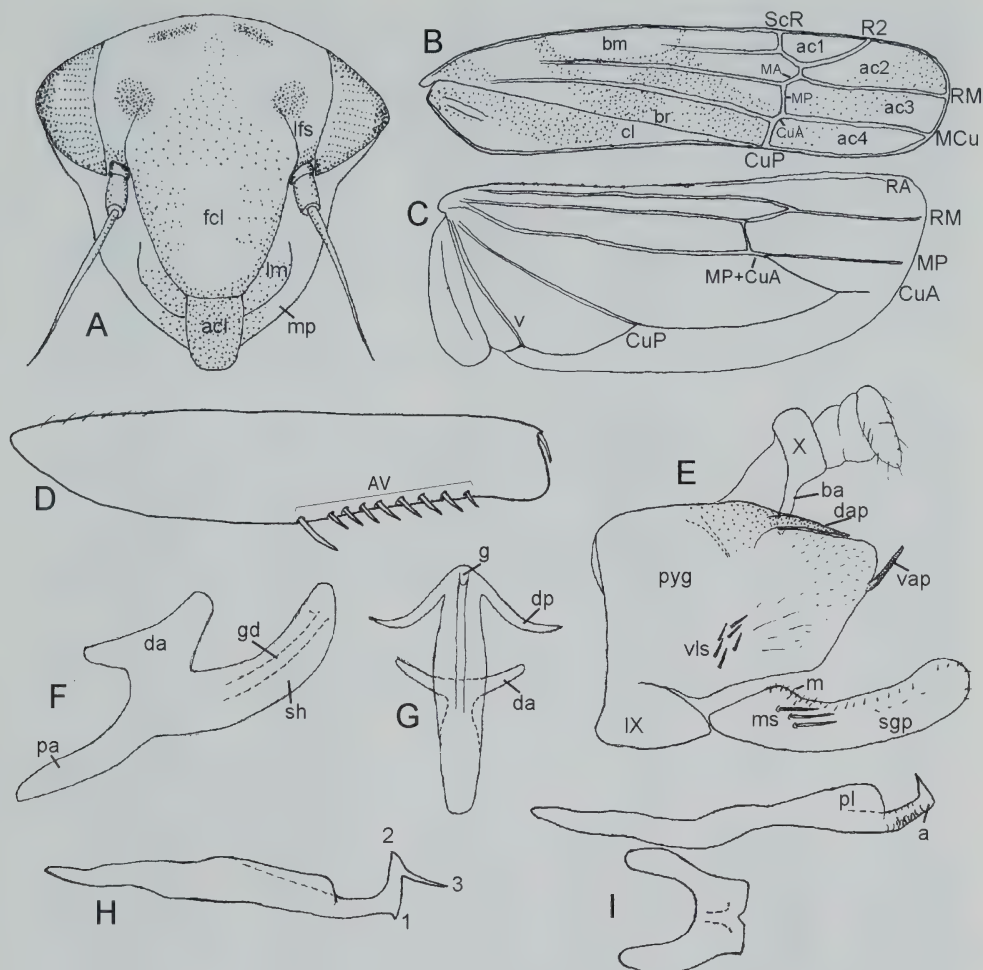


Figure 1. Erythroneurini morphology. A, *Mexigina oculata* (McAtee), head, anterior view; B–C, *Erythroneura kanwakae* Beamer, forewing (B) and hind wing (C); D, *M. oculata*, front femur, anterior view; E, *Zyginama ritana* (Beamer), male genital capsule, lateral view; F, *Z. nuda* (Knull and Auten), aedeagus, lateral view; G, *Neozygina ceonothana* (Beamer), aedeagus, posterior view; H, *Nelionidia moyai*, n. sp., male style, ventrolateral view, distal points numbered as shown; I, *Amazygina decaspina*, n. sp., left style and connective, ventral view. Abbreviations: a, apophysis; ac, apical cell; acl, anteclypeus; ba, basolateral arm; bm, brochosome field; br, brachial cell; cl, clavus; da, dorsal apodeme; dap, dorsal appendage; dp, distal process; fcl, frontoclypeus; g, gonopore; gd, gonoduct; lfs, lateral frontal suture; lm, lorum; m, marginal setae; mp, maxillary plate; ms, macrosetae; pa, preatrium; pl, preapical lobe; pyg, pygofer; sgp, subgenital plate; sh, shaft; v, vannal vein; vap, ventral appendage; vls, ventrolateral setae.





Figure 2. Dorsal habitus. A, *Erythridula insigna* (Beamer and Griffith); B, *Erythroneura corni* Robinson; C, *Eratoneura dira* (Beamer); D, *Erasmoneura vulnerata* (Fitch); E, *Hymetta trifasciata* (Say); F, *Aztegina punctinota*, n. sp.; G, *Hepzygina milleri* (Beamer); H, *Illinigina illinoiensis* (Gillette); I, *Mexigina oculata* (McAtee); J, *Nelionidia elliptica* n. sp.; K, *Neoimbecilla kiperi* (Beamer); L, *Neoimbecilla latiplata*, n. sp.; M, *Neozygina apacha* (Baker); N, *Rossmoneura tecta* (McAtee); O, *Zyginama ritana*; P, *Amazygina compressa*, n. sp.; Q, *Hamagina spinigera*, n. sp.; R, *Napogina sinuata*, n. sp.



Figure 3. A-S, forewing: A, *Erythridula obliqua* (Say); B, *Eratoneura ligata* (McAtee); C, *Eratoneura maculata* (Gillette); D, *Erasmoneura vulnerata* (Fitch); E, *Hymetta balteata* McAtee; F, *Aztegina punctinota*, n. sp.; G, *Hepzygina milleri* (Beamer); H, *Illinigena illinoiensis* (Gillette); I, *Mexigina oculata* (McAtee); J, *Neoimbecilla kiperi* (Beamer); K, *Nelionidia moyai*, n. sp.; L, *Nelionidia pueblensis*, n. sp.; M, *Nelionidia pallescens*, n. sp.; N, *Neozygina ceonothana* (Beamer); O, *Zyginama ritana* (Beamer); P, *Amazygina decaspina*, n. sp.; Q, *Hamagina spinigera*, n. sp.; R, *Perugina denticula*, n. sp.; S, *Spinigina hirsuta*, n. sp. T-CC, hind wing: T, *Erythridula obliqua*; U, *Erasmoneura vulnerata*; V, *Aztegina punctinota*; W, *Illinigena illinoiensis*; X, *Mexigina oculata* (unusual specimen with closed apical cell); Y, *Neoimbecilla kiperi*; Z, *Nelionidia pallescens*; AA, *Neozygina ceonothana*; BB, *Zyginama ritana*; CC, *Amazygina decaspina*.



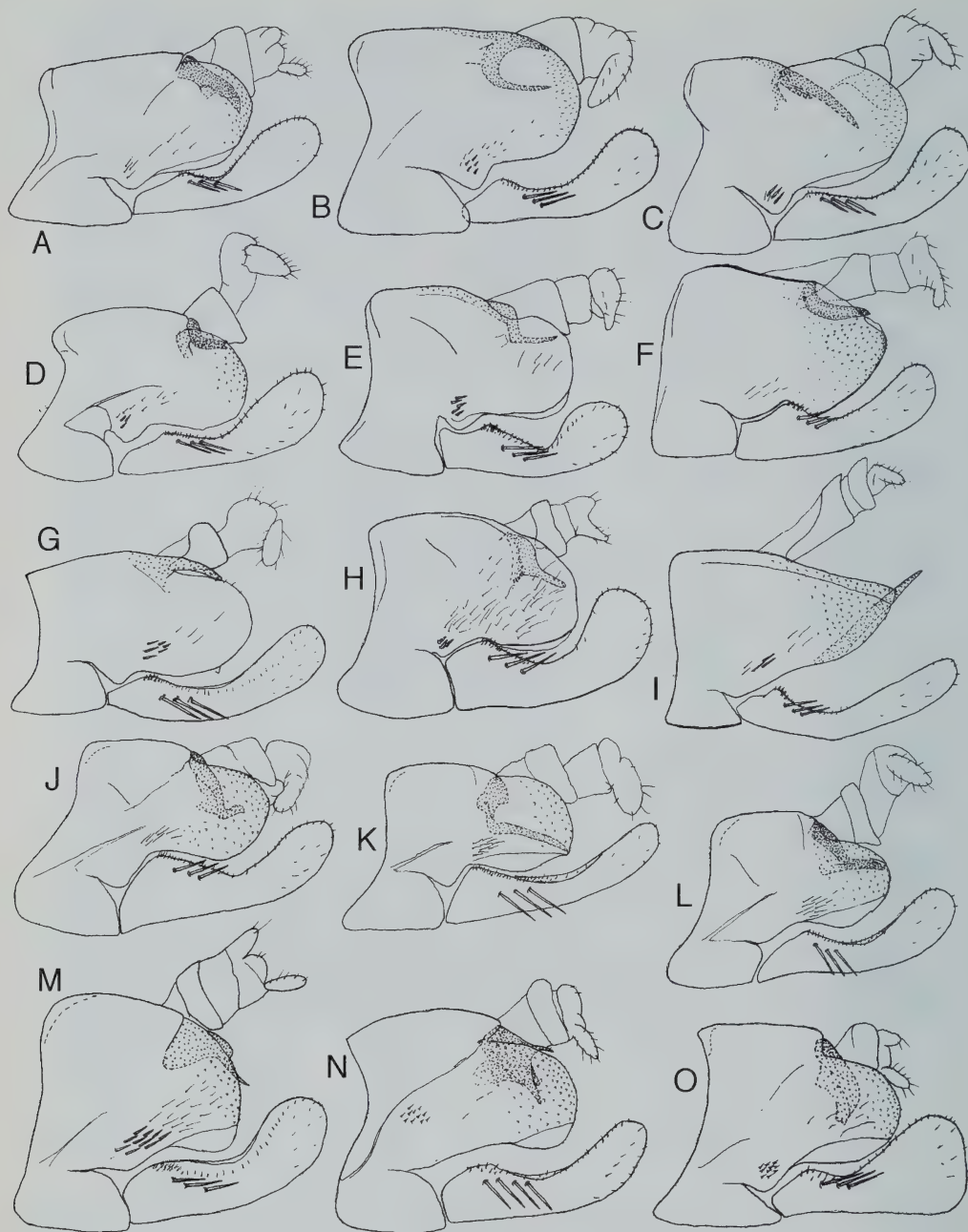


Figure 4. Male genital capsule, lateral view. A, *Erythrídula obliqua*; B, *Erythroneura comes* (Say); C, *Eratoneura maculata*; D, *Erasmoneura vulnerata*; E, *Hymetta balteata* McAtee; F, *Aztegina punctinota*, n. sp.; G, *Hepzigina milleri*; H, *Illinigina illinoiensis*; I, *Mexigina oculata*; J, *Nelionidia elliptica*; K, *Nelionidia moyai*; L, *Nelionidia pallescens*; M, *Nelionidia pueblensis*; N, *Neoimbecilla kiperi*; O, *Neoimbecilla latiplata*.



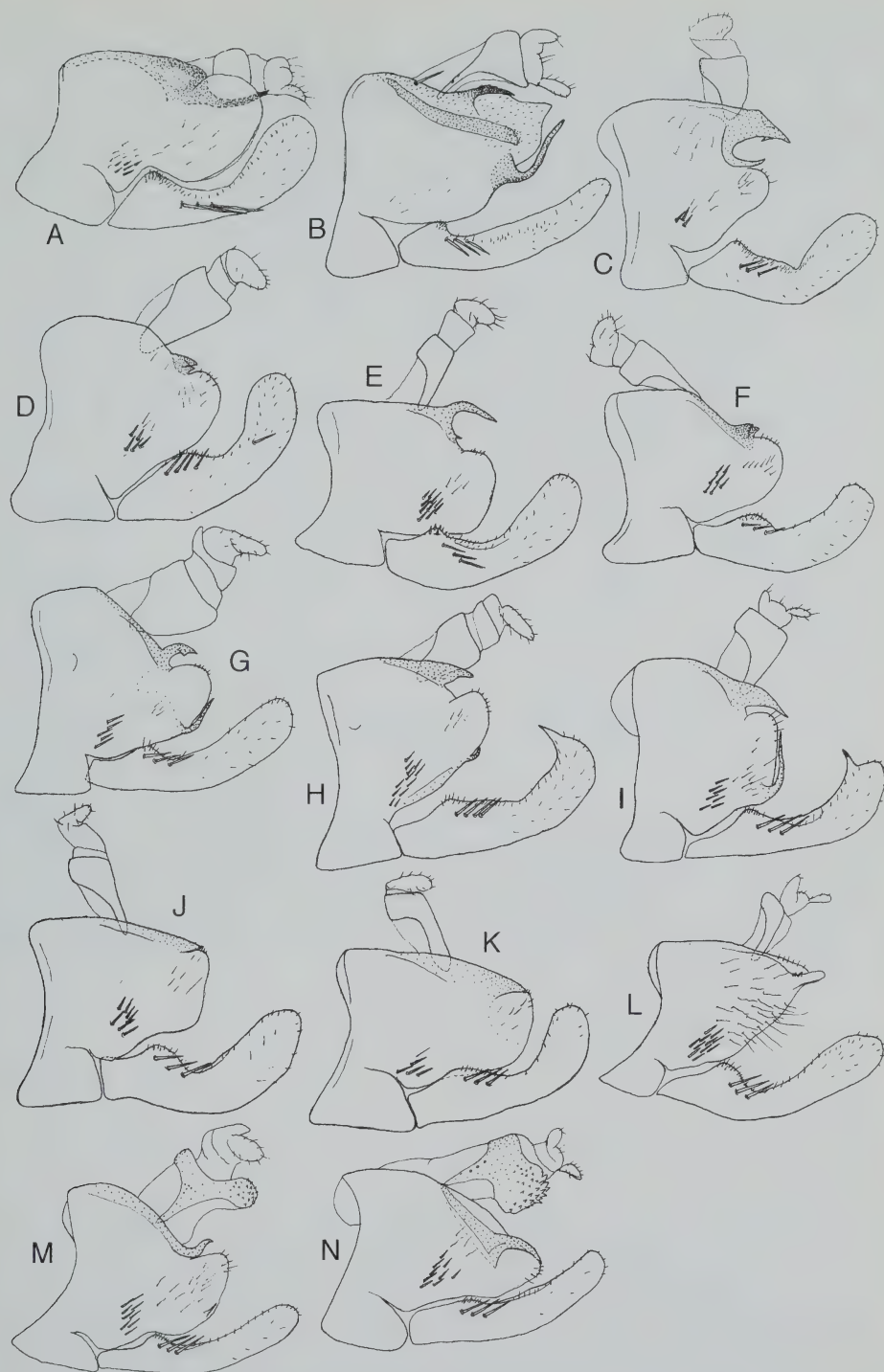


Figure 5. Male genital capsule, lateral view. A, *Rossmoneura tecta*; B, *Neozygina ceonothana*; C, *Amazygina chela*, n. sp.; D, *Amazygina compressa*, n. sp.; E, *Amazygina depressa*, n. sp.; F, *Amazygina decaspina*, n. sp.; G, *Hamagina pascoensis*, n. sp.; H, *Hamagina serrata*, n. sp.; I, *Hamagina spinigera*, n. sp.; J, *Napogina recta*, n. sp.; K, *Napogina sinuata*, n. sp.; L, *Perugina denticula*, n. sp.; M, *Spinigina hirsuta*, n. sp.; N, *Spinigina quadrispinosa*, n. sp.

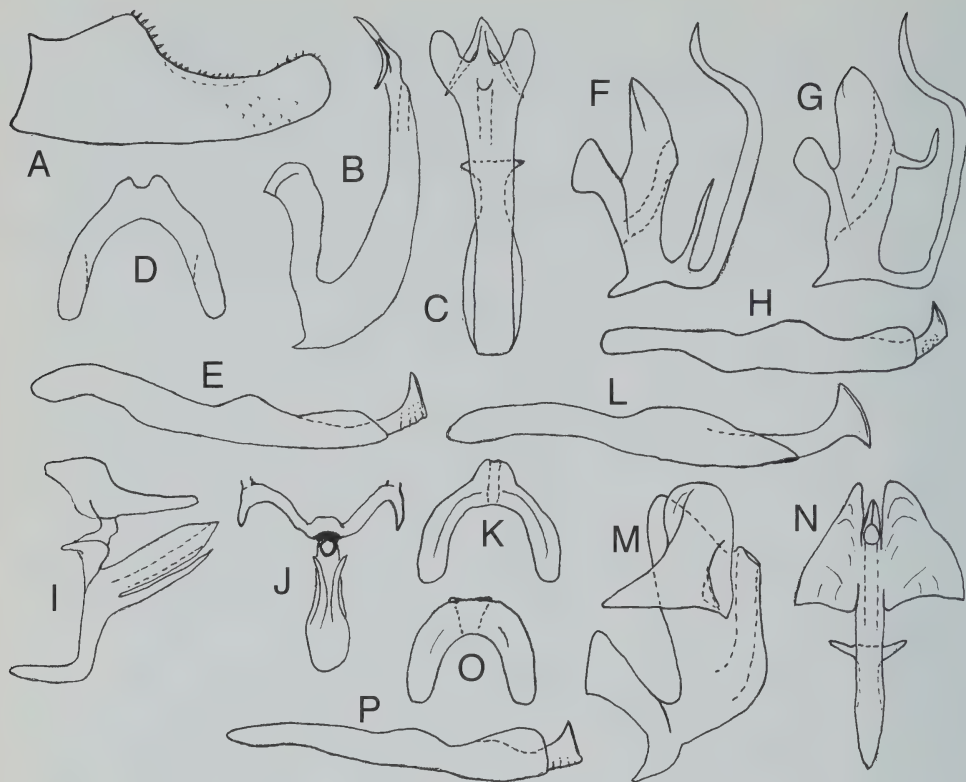


Figure 6. Male genitalia. A–D, *Aztegina punctinota*: A, subgenital plate, ventral view; B, aedeagus, lateral view; C, same, posterior view; D, connective, ventral view. E, style, lateral view; F, *Hepzygina milleri*, aedeagus, lateral view. G–H, *Hepzygina aprica*: G, aedeagus, lateral view; H, style, lateral view. I–L, *Illinigina illinoiensis*: I, aedeagus and dorsal pygofer appendage, lateral view; J, same, posterior view; K, connective, ventral view; L, style, lateral view. M–P, *Mexigina oculata*: M, aedeagus, lateral view; N, same, posterior view; O, connective, ventral view; P, style, lateral view.

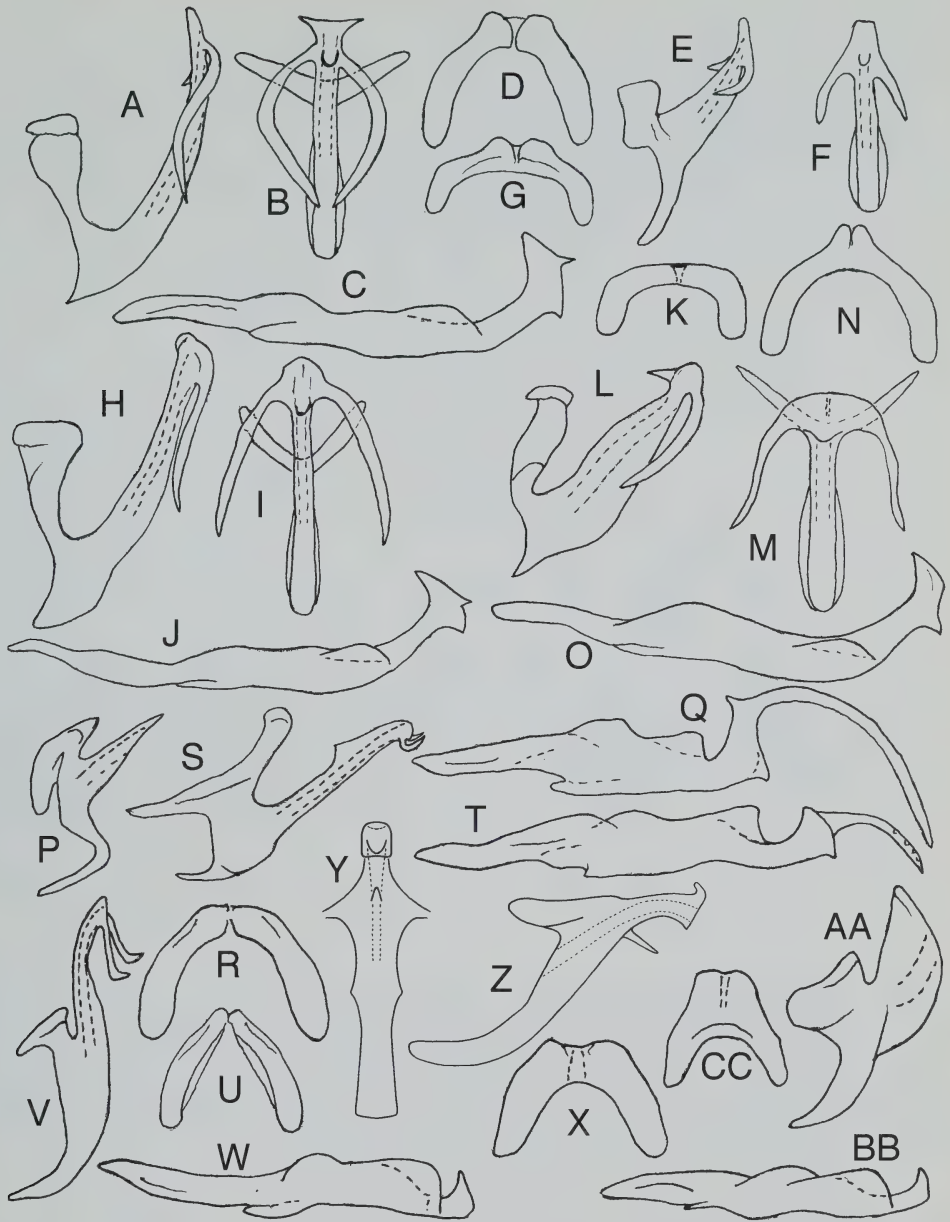


Figure 7. Male genitalia. A–C, *Nelionidia elliptica*: A, aedeagus, lateral view; B, same, posterior view; C, style, lateral view; D, connective, ventral view. E–G, *Nelionidia moyai*: E, aedeagus, lateral view; F, same, posterior view; G, connective, ventral view. H–K, *Nelionidia pallescens*: H, aedeagus, lateral view; I, same, posterior view; J, style, lateral view; K, connective, ventral view. L–N, *Nelionidia pueblensis*: L, aedeagus, lateral view; M, same, posterior view; N, connective, ventral view; O, style, lateral view. P–R, *Neoimbecilla latiplata*: P, aedeagus, lateral view; Q, style, ventral view; R, connective, ventral view. S–U, *Neoimbecilla kiperi*: S, aedeagus, lateral view; T, style, ventral view; U, connective, ventral view. V–X, *Neozygina ceanothana*: V, aedeagus, lateral view; W, style, ventrolateral view; X, connective, ventral view. Y–Z, *Rossmoneura tecta*, aedeagus, posteroventral and lateral views, respectively. AA–CC, *Zygina ritana*: AA, aedeagus, lateral view; BB, style, ventral view; CC, connective, ventral view.



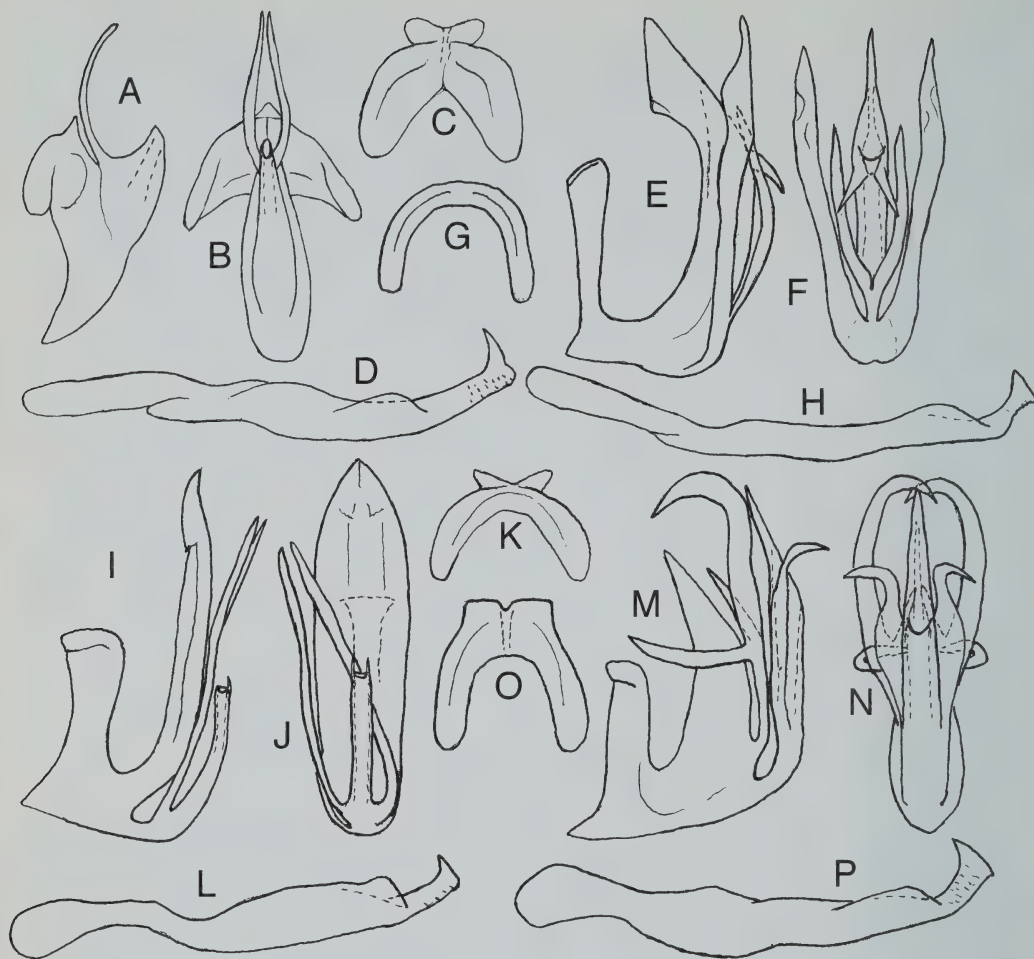


Figure 8. *Amazygina*, male genitalia. A–D, *Amazygina chela*: A, aedeagus, lateral view; B, same, posterior view; C, connective, ventral view; D, style, lateral view. E–H: *Amazygina compressa*: E, aedeagus, lateral view; F, same, posterior view; G, connective, ventral view; H, style, lateral view. I–L, *Amazygina depressa*: I, aedeagus, lateral view; J, same, posterior view; K, connective, ventral view; L, style, lateral view; M–P, *Amazygina decaspina*: M, aedeagus, ventral view; N, same, posterior view; O, connective, ventral view; P, style, lateral view.

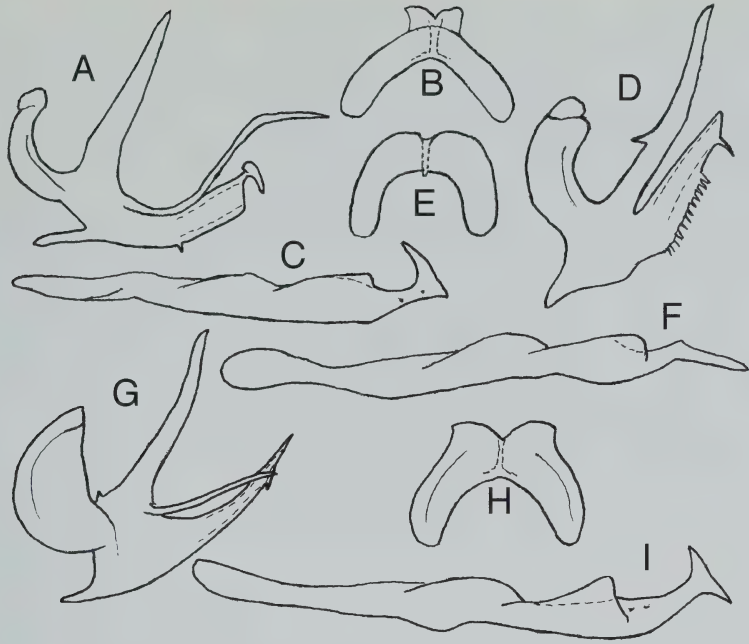


Figure 9. *Hamagina*, male genitalia. A–C, *Hamagina pascoensis*: A, aedeagus, lateral view; B, connective, ventral view; C, style, ventral view. D–F, *Hamagina serrata*: D, aedeagus, lateral view; E, connective, ventral view; F, style, ventrolateral view. G–I, *Hamagina spinigera*: G, aedeagus, lateral view; H, connective, ventral view; I, style, ventral view.

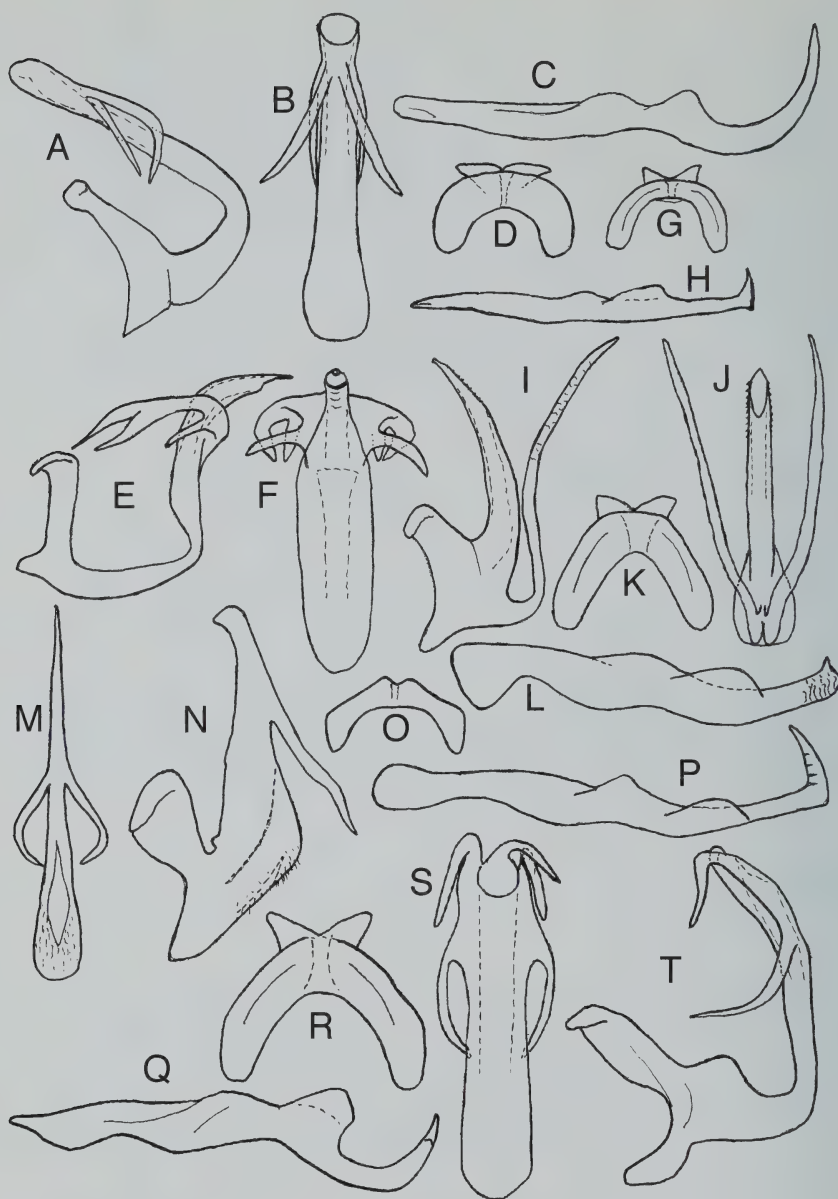


Figure 10. Male genitalia. A-D, *Napogina recta*: A, aedeagus, lateral view; B, same, posterior view; C, style, ventral view; D, connective, ventral view. E-H, *Napogina sinuata*: E, aedeagus, lateral view; F, same, posterior view; G, connective, ventral view; H, style, ventrolateral view. I-L, *Perugina denticula*: I, aedeagus, lateral view; J, same, posterior view; K, connective, ventral view; L, style, ventrolateral view. M-P, *Spinigina hirsuta*: M, aedeagus, lateral view; N, same, posterior view; O, connective, ventral view; P, style, ventrolateral view. Q-T, *Spinigina quadrispinosa*: Q, style, ventral view; R, connective, ventral view; S, aedeagus, posterior view; T, same, lateral view.



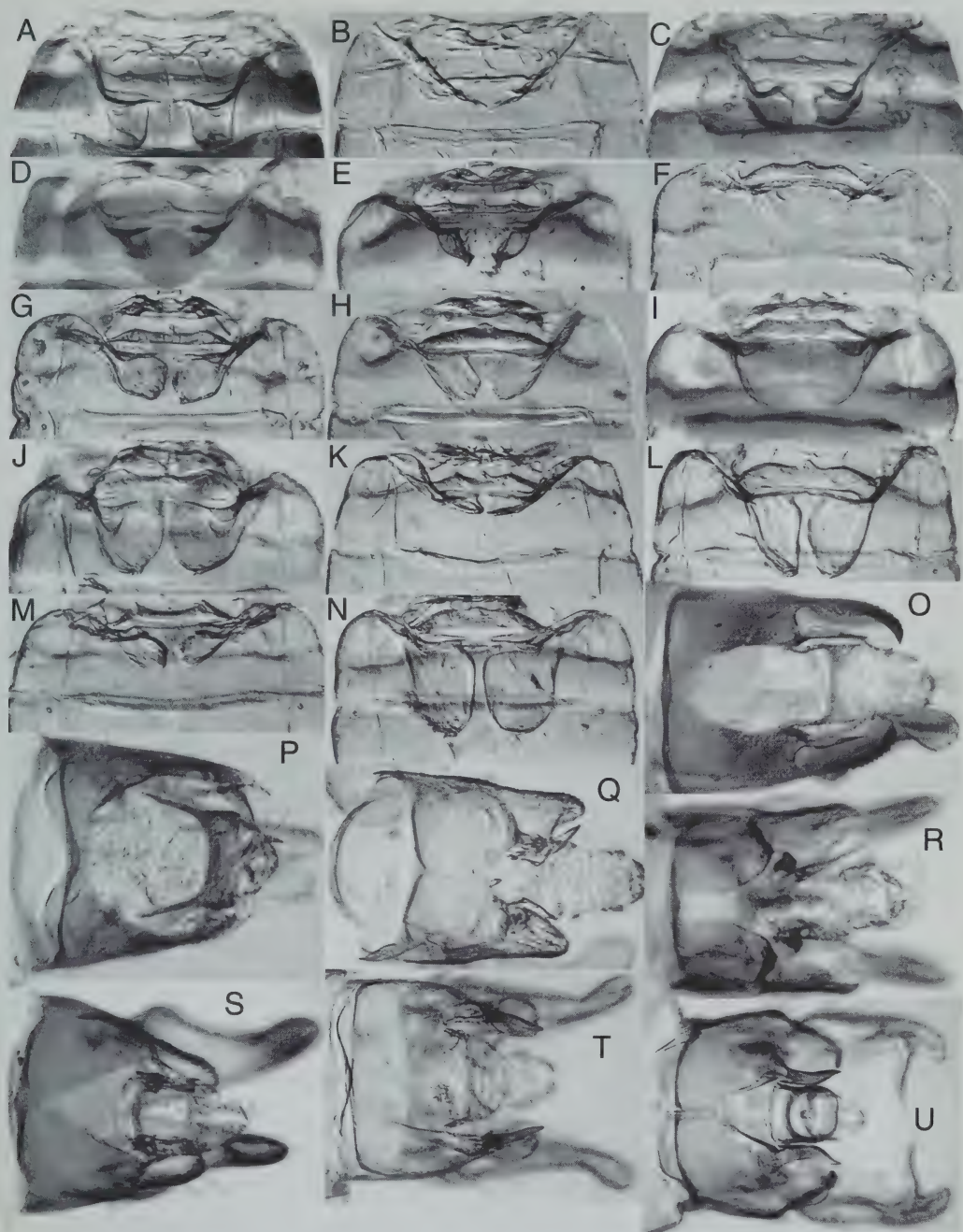


Figure 11. Male abdomen. A–N, base of abdomen ventral view: A, *Aztegina punctinota*; B, *Mexigina oculata*; C, *Neozygina ceonothana*; D, *Nelionidia pueblensis*; E, *Amazygina chela*; F, *Amazygina compressa*; G, *Amazygina depressa*; H, *Amazygina decaspina*; I, *Hamagina pascoensis*; J, *Hamagina serrata*; K, *Hamagina spinigera*; L, *Napogina recta*; M, *Perugina denticula*; N, *Spinigina hirsuta*. O–U: genital capsule, dorsal view: O, *Aztegina punctinota*; P, *Neozygina ceonothana*; Q, *Nelionidia elliptica*; R, *Nelionidia moyai*; S, *Nelionidia pueblensis*; T, *Amazygina depressa*; U, *Hamagina spinigera*.

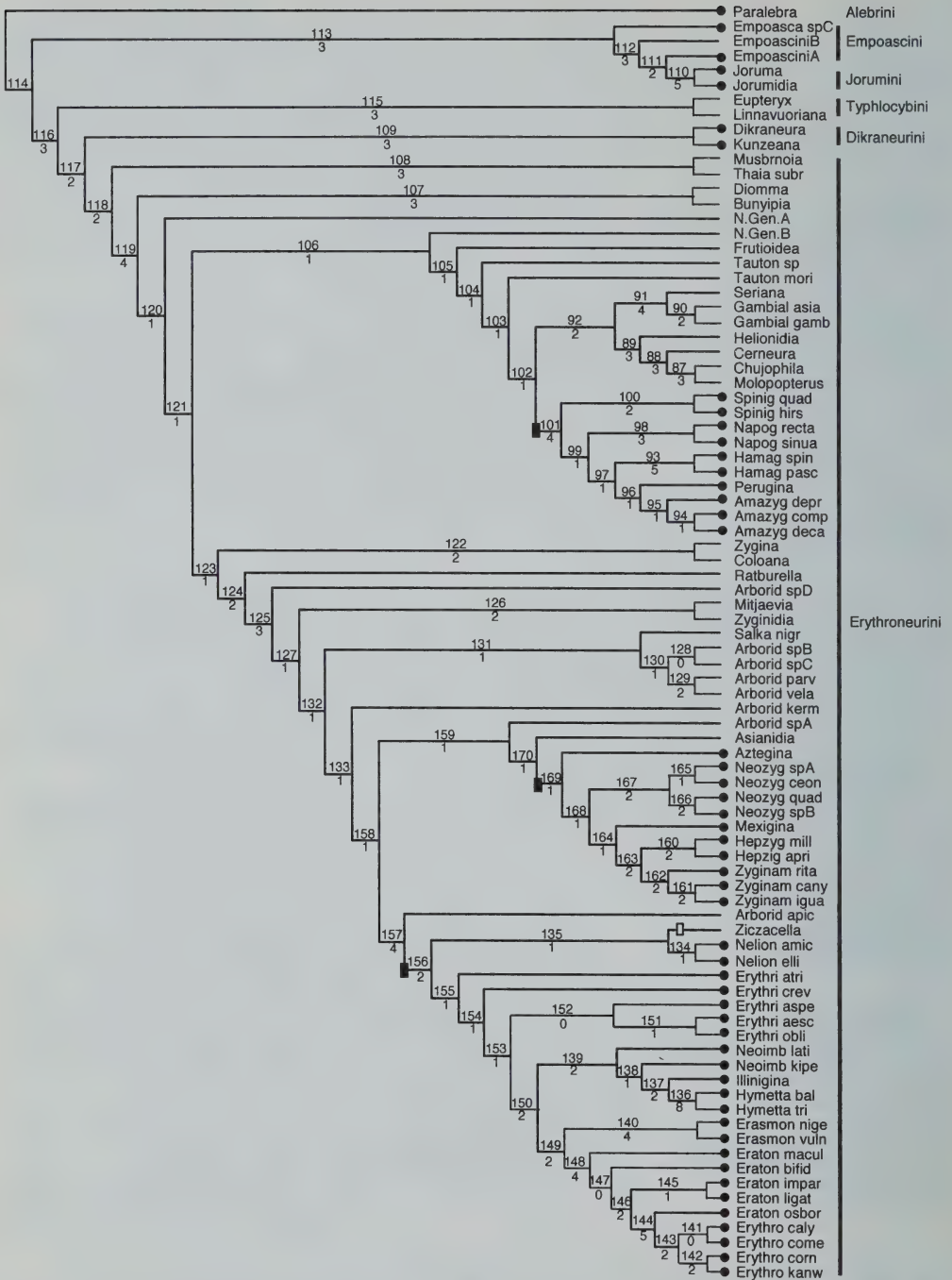


Figure 12. One of 24 equally parsimonious trees from phylogenetic analysis of 100 morphological characters. Apomorphies for numbered nodes and terminal taxa are given in Appendix D. Decay indices are given below the branches; nodes with decay index = 0 collapsed on the strict consensus tree. Black circles at branch tips indicate New World taxa. Black rectangles on internal nodes indicate separate invasions of Erythroneurini into the New World, based on accelerated transformation optimization. The clear rectangle subtending *Ziczacella* indicates a “reversal” from New to Old World. This scenario is equally parsimonious to one in which separate invasions of the New World by the ancestor of *Nelionidia* and of the clade comprising *Erythridula atrimucronata* occurred.





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SURVEY

# Vegetation and Flora of the Sand Deposits of the Mississippi River Valley in Northwestern Illinois

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## ABSTRACT

This study was undertaken to determine vascular plant species composition, vegetation structure, and floristic quality of the major plant communities in the windblown sand deposits of northwestern Illinois during the growing seasons of 2002 through 2005. The major plant communities of the Ayers Sand Prairie Nature Preserve in Carroll County, Big River State Forest in Henderson County, Lost Mound Unit of the Upper Mississippi River Wildlife and Fish Refuge in Carroll and Jo Daviess counties, and the Thomson-Fulton Sand Prairie Nature Preserve located in Whiteside County were examined and the importance values determined for the plant species present. Located on broad terraces of the Mississippi River, these nature preserves and natural areas are remnants of a larger grassland/savanna/forest complex that contained extensive marsh; wet, mesic, and dry sand prairie; sand savanna; and sand forest communities. Most of the sand deposits are now cultivated and the original vegetation is found only in protected remnants, some of which are relatively large. The mature dry sand prairies were dominated by *Schizachyrium scoparium*; other important species were *Opuntia macrorhiza*, *Dichanthelium villosissimum*, *Ambrosia psilostachya*, and *Tephrosia virginiana*. Other assemblages of prairie and exotic species were encountered in successional sand prairie communities. Generally, the mature prairie communities in these preserves and natural areas had 35 or more species present in the study plots. Savanna and closed canopy forest communities were also examined. The dry sand savannas were dominated by *Quercus velutina* and *Q. marilandica*, dry sand forests were dominated by *Q. velutina*, and dry-mesic sand forests were dominated by *Q. alba* and *Q. velutina*.

## INTRODUCTION

Glacial outwash, windblown sand deposits are common in the northern half of Illinois due to erosional events associated with Wisconsin glacialiation (Willman and Frye 1970, Schwegman 1973, King 1981). The most extensive are the Kankakee sand deposits in northeastern Illinois and the Illinois River sands of Cass, Mason, and Tazewell counties in central Illinois. Numerous smaller sand deposits also occur, including the sands along the upper Mississippi River and its tributaries, the Green River Lowlands sand deposits of Lee and Henry counties in northwestern Illinois, and the Chicago Lake plain and beaches along Lake Michigan in northeastern Illinois.

These sand deposits, named the Parkland Sand or the Parkland Formation, consist of windblown sand in dunes and in sheetlike deposits between and bordering the dunes (Willman and Frye 1970). The dunes are usually found on terraces along the major river valleys in the northern half of Illinois, and consist of medium-grained sands that are sorted by wind from the underlying glacial outwash. These sands were reworked by wind forming the dune and swale topography characteristic of these deposits. Dunes 6 to 12 meters high are common and occasional dunes to 30 m tall are encountered (Gleason 1910).

Extensive glacial outwash, windblown sand deposits are scattered throughout the lowlands of the Mississippi River in northwestern Illinois (Fig. 1). Referred to as the Mississippi River Section of the Illinois River and Mississippi River Sand Areas Natural Division, these scattered deposits occur from Jo Daviess County south to Henderson County (Schwegman 1973). Some of these deposits were formed when glacial lakes (Lake Milan and Lake Cordova) in Carroll, Henry, Rock Island, and Whiteside counties drained (Fig. 1). Others were deposited during flood events during the retreat of the Wisconsin Glacier when moraines and ice dams were breached and glacial lakes to the north of Illinois drained (Willman and Frye 1970).

Dry habitats are characteristic of sand deposits, and the commonly associated species are those adapted to xeric conditions. However, plant communities of sand deposits are extremely diverse and include sand ponds (McClain et al. 1997), marshes and sedge meadows (Handel et al. 2003, Feist et al. 2006), prairies (Handel et al. 2003, McClain et al. 2003, 2004, Phillippe et al. 2004), savannas and woodlands (McDowell et al. 1983, Johnson and Ebinger 1992, 1995), closed forests (Jenkins et al. 1991, Coates et al. 1992, McClain et al. 2002), and flatwoods (McDowell et al. 1983).

Some of the most comprehensive early work completed on the vegetation of Illinois sand deposits was undertaken in the early 1900s by Dr. Henry Allen Gleason, an ecologist and plant geographer then at the Illinois Natural History Survey, and by Arthur G. Vestal, a botanist at the University of Illinois (Hart and Gleason 1907, Gleason 1910, Vestal 1913). These authors described the principal plant communities and discussed the animals associated with these sand deposits, particularly the insects.

Except for the early work by Gleason (1910), little has been published concerning the vegetation of sand deposits along the Upper Mississippi River valley in northwestern Illinois. Though most of these scattered sand deposits are now under cultivation, a fairly extensive preserve system has maintained some of this former diversity. The present study was undertaken to determine vascular plant species composition, vegetation structure of the different plant communities based on the life forms of the species present, and the floristic quality of the major plant communities of the nature preserves and other natural areas located in the windblown sand deposits of the Mississippi River Section of the Illinois River and Mississippi River Sand Areas Natural Division in northwestern Illinois.

## STUDY SITES

All of the study sites are located within 150 km of each other, and are within a few km of the Mississippi River (Fig. 1). The climate associated with these sand deposits is continental with warm summers and cold winters. Based on weather data from Dixon, Illinois, 50 km east of the Mississippi River near the middle of the study area, mean annual precipitation is 94.7 cm, with June having the highest rainfall (12.4 cm). Mean annual temperature is 8.5°C with the hottest month being July (average of 22.3°C), and the coldest January (average of -7.9°C). The average number of frost-free days is 161 (Midwestern Regional Climate Center 2005).

**Lost Mound Unit of the Upper Mississippi River Wildlife and Fish Refuge:** Lost Mound is located in northwest Carroll and southwest Jo Daviess counties on the former Savanna Army Depot (42.2410°N, -90.3380°W [WGS84/

NAD83]). Gleason (1910), in his classic monograph "Vegetation of the Inland Sand Deposits of Illinois," first described this extensive prairie, which was known as "The Prairie" by local residents. Little of the area was destroyed by cultivation, as grazing was the primary agricultural use of the area. In 1918 the U.S. army purchased most of "The Prairie" to use as an artillery test range. While ownership by the army prevented the large-scale conversion of this area to row crops, the landscape was damaged with the construction of warehouses and other structures that were used to store munitions, and the roads and railroads used to transport them.

The army's mission required preventing wildfires in the extensive remaining prairie. The army restricted the potential for fires by introducing grazing to the area beginning in the late 1940s. Whereas cattle were the primary means of reducing vegetation cover, sheep were used for a time in the early 1950s. Recent cattle grazing leases typically began in late March and extended until November, with 1,000 to 1,200 cattle reducing the vegetation to a lawnlike condition (Robertson et al. 1997). Areas where watering tanks were established had even greater disturbance to the surrounding vegetation, often with extensive areas of bare sand exposed. Where cattle had access to the Mississippi River, side slopes of the sand bluffs were rutted and eroded. Also, changes in the river's hydrology to maintain the navigational channel, have created higher water levels that caused additional bluff erosion and sloughing. Cattle helped maintain some of the blowout communities by increasing disturbance. Recent grazing leases also had provisions to improve the grasslands. *Juniperus virginiana* (red cedar) and other brush were removed, and some herbaceous vegetation was planted. As part of this "improvement" program, some areas were seeded with a no-till drill to Eurasian cool-season grasses and adventive legumes, particularly *Bromus inermis* (awnless brome grass) and *Trifolium arvense* (rabbit-foot clover).

Even with the disturbances, the Illinois Natural Areas Inventory recognized most of the Savanna Army Depot as a statewide significant natural area because of the size of the prairie remnant, the potential for recovery, and the many rare plants and animals present (White 1978). Bowles and Jones (1995) noted the locations of numerous state-listed plants and



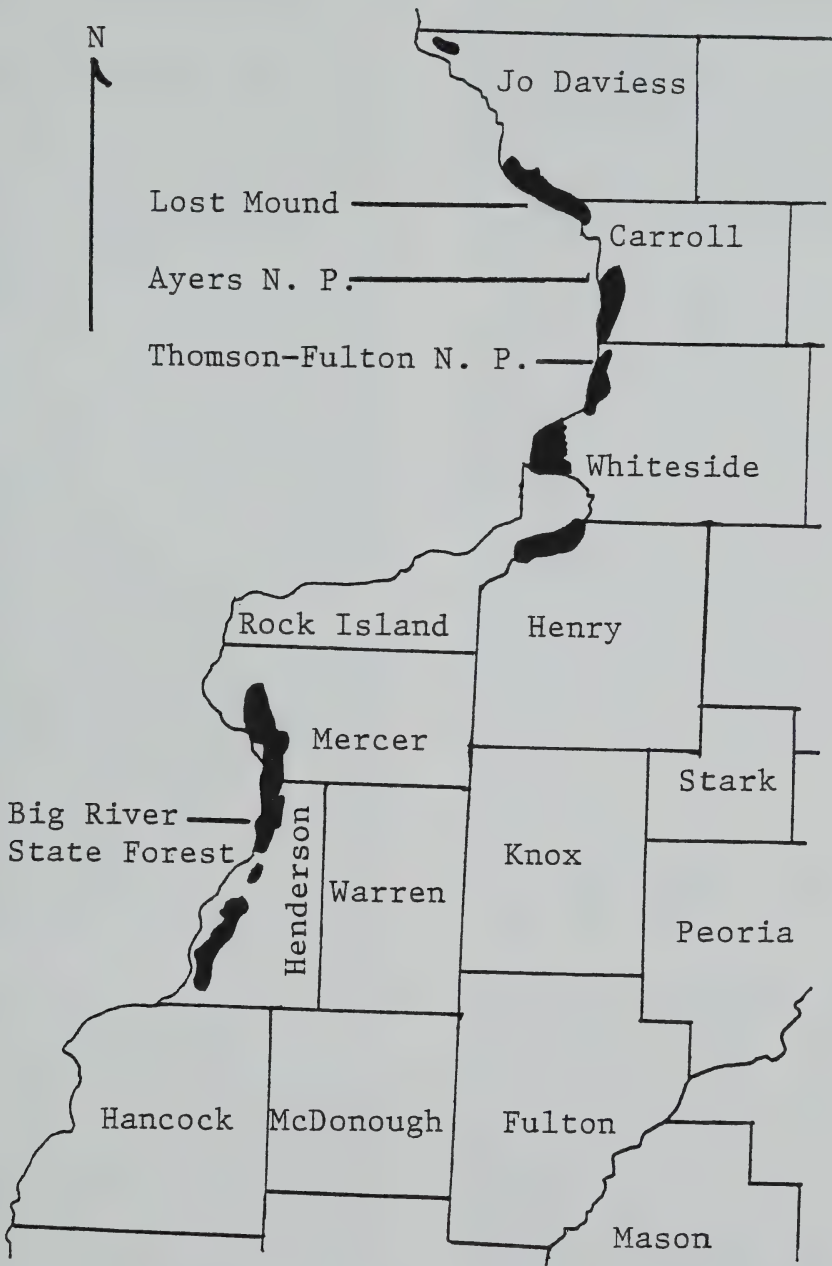


Figure 1. Distribution of sand deposits along the Mississippi River in northwestern Illinois from Jo Daviess County to Henderson County, Illinois. The general location of the four natural areas and nature preserves studies are also included.

prairies of high natural quality on the depot. As a result, staff of the Illinois Department of Natural Resources persuaded the army to fence some areas to exclude cattle, reduce the grazing period, and decrease the number of cattle on the depot. Grazing ceased in the late 1990s as the military mission was ended at the depot. The land first was transferred to the U.S. Fish and Wildlife Service in 2003. Some of the prairie parcels sampled have been transferred to the Illinois Department of Natural Resources and the Jo-Carroll Local Redevelopment Authority in later years.

The major soil type of Lost Mound is Sparta loamy sand that developed under prairie vegetation. This soil is found on flat to sloping areas, is excessively drained, and consists of deep, dark brown, friable, coarse sand that is underlain by fine loose yellow sand that is often exposed in blowouts (Tegeler 1996). The savanna soils are mostly on steep slopes and are classified as Chelsea loamy sands, which are excessively drained, dark grayish brown in color, and relatively thin; while the nearly level upland forest soils are classified as Bloomfield loamy fine sand and have a similar structure. The floodplain forest soils at Lost Mound are Birds silt loam, which are nearly level, poorly drained, and dark gray-brown in color.

**Ayers Sand Prairie Nature Preserve:** This preserve is located in northwestern Carroll County about 3 km south of Savanna (SE1/4 S24 T24N R3E; 42.0535°N, -90.1051°W [WGS84/NAD83]). This 46-ha area was dedicated as an Illinois Nature Preserve in 1974. Since dedication the preserve has been recovering from past grazing, off-road vehicle use, cultivation, and other disturbances. The southeastern and northwestern thirds of the preserve are recovering from heavy grazing and cultivation. Parts of the cultivated areas are rapidly reverting to sand prairie vegetation, while *Bromus inermis* and other cool-season introduced grasses dominate an extensive area in the southeastern part of the preserve. Some blowouts are present in the preserve, though most are now revegetated. The southwestern third of the preserve contains some high-quality dry sand prairie. This area is probably still recovering from past grazing, but was not cultivated. The Illinois Natural Area Inventory considered most of the preserve to be "Grade C" dry sand prairie due to extensive disturbances, though

parts of the southwestern section were listed as "Grade B" with a few small areas of "Grade A" (White 1978). The soils of the preserve are Sparta loamy sands (Ray et al. 1975).

### **Thomson-Fulton Sand Prairie Nature**

**Preserve:** This preserve is located in extreme northwestern Whiteside County about 6 km northeast of Fulton, Illinois (SW1/4 S1 and SE1/4 S2 T22N R3E; 41.9253°N, -90.1113°W [WGS84/NAD83]), immediately south of the Carroll/Whiteside County line. It is a small part of the Thomson Sand Area that extends north into Carroll County. In Whiteside County this sand deposit covers nearly 85 km<sup>2</sup> (Smith et al. 1928). The preserve contains about 15 ha of sand prairie that are currently recovering from past grazing, off-road vehicle use, cultivation, and other disturbances. In portions of both the southern and northern parts of this prairie, several ha were plowed and planted to watermelons the year before being dedicated as a preserve by the Illinois Department of Conservation in 1970. This cultivated area is reverting to sand prairie vegetation. Disturbance by off-road vehicles increased the size and number of blowouts in the preserve. These areas are now recovering, many being revegetated, but some contain moving sand. Also, pines that were planted in parts of the prairie prior to acquisition, have been mostly removed. The Illinois Natural Area Inventory considered the area to be mostly "Grade C" dry sand prairie due to extensive disturbances (White 1978). The soils of the preserve are mostly Sparta loamy sand (Sabata 1995).

**Big River State Forest:** This state forest, which contains a few natural areas, is located in northwestern Henderson County, about 8 km north of Oquawka (S24, S25, S36 T12N R5W; 40.9920°N, -90.9205°W [WGS84/NAD83]). Two natural areas within the state forest were studied; a dry sand prairie (NW1/4 S36) and a degraded dry sand savanna (SW1/4 S25). Both sites have been subjected to past disturbances. The dry sand prairie was heavily grazed in the past and pines were planted along the east edge. The dry sand savanna was probably clear-cut soon after settlement and has been subjected to more recent cutting and fire suppression. The Illinois Natural Area Inventory considered most of the dry sand prairie to be of "Grade B" quality, while the dry sand savanna was listed as

"Grade C" due to the young trees of small size, fire suppression, and other disturbances (White 1978). The soils of the natural areas studied are light colored Plainfield sand and medium-dark colored Oquawka sand that are water-deposited sands of the Mississippi River terrace that have been reworked by wind (Veale and Wascher 1956).

## MATERIALS AND METHODS

### Vascular Plant Species and Community

**Types:** The natural areas studied were visited a minimum of five times each year throughout the growing seasons of 2002 through 2005, except for the Lost Mound Unit, which was extensively studied on numerous earlier trips during the growing seasons of 1996 and 1997 by some of the authors (Robertson et al. 1997). Voucher specimens of each plant species were collected, identified, and deposited in the herbarium of the Illinois Natural History Survey, Champaign, Illinois (ILL), and the Stover-Ebinger Herbarium of Eastern Illinois University, Charleston, Illinois (EIU). The species encountered are listed in Appendix I. This list of taxa includes the citation of voucher specimens of nearly all species that have been found in the natural areas studied, as well as a few taxa that were observed but not collected. The list also includes a few species reported by the Illinois Natural Area Inventory (INAI) for which vouchers could not be located. Criteria for designating adventive (non-native) species followed Mohlenbrock (2002), Gleason and Cronquist (1991), and Taft et al. (1997). Nomenclature follows Mohlenbrock (2002). We recorded the location of threatened and endangered plant species listed by Herkert and Ebinger (2002).

The plant communities encountered were described, for the most part, using the classification system of White and Madany (1978). All of the sand prairie communities examined during the present study would be described as various successional stages of a dry sand prairie, including the blowout and blowing sand communities discussed below. In some instances we added modifiers in parenthesis to indicate successional trends, and sometimes the dominant species when discussing a particular community. We consider a mature-to-late successional sand prairie to be equivalent to Grades A and B used by the Illinois Natural Area Inventory (INAI), while successional sand prairie to be equivalent to a low Grade B or C (White 1978). The INAI

grading criteria are based on the perceived successional state of the vegetation with Grade A (essentially not degraded [high floristic quality]) to Grade E (highly disturbed [i.e., cropland]).

**Ground Layer Sampling:** In the late summers of 2004 and 2005 transects were located randomly along cardinal compass directions within the sand prairie communities studied. These transects were located using aerial photographs and ground observation to ensure that they did not cross community boundaries. Within each community a 50-m-long transect was located. Along each transect, 1-m<sup>2</sup> quadrats were alternately located at 1-m intervals ( $n=50/\text{transect}$ ). A random numbers table was used to determine the number of meters (0 to 9) a quadrat was located from the transect line. In some areas (Ayers Sand Prairie Nature Preserve, Thomson-Fulton Sand Prairie Nature Preserve, Big River State Forest) more than one 50-m transect was completed for each habitat type. Only the first transect completed in each habitat type was used in the calculations in this paper. Species cover was determined using the Daubenmire (1959) Cover Class System as modified by Bailey and Poulton (1968). The modified Daubenmire cover scale is as follows: Class 1 = 0 to 1%; Class 2 = >1 to 5%; Class 3 = >5 to 25%; Class 4 = >25 to 50%; Class 5 = >50 to 75%; Class 6 = >75 to 95%; Class 7 = >95 to 100%. Importance Value (IV) was determined by summing relative cover and relative frequency (total possible=200).

**Overstory Sampling:** Savanna and forest communities at Lost Mound and Big River were studied in the late summer of 2005. These areas were surveyed by dividing a portion of each savanna or forest community into contiguous quadrats 25 m on a side. These sample quadrats were located near the central part of each study area and more than 50 m from the nearest woodland edge. All living and dead-standing woody individuals  $\geq 10.0$  cm dbh were identified and their diameters recorded. From these data, living-stem density (stems/ha), basal area (m<sup>2</sup>/ha), relative density, relative dominance, importance value (IV), and average diameter (cm) were calculated for each species. Determination of the IV follows the procedure used by McIntosh (1957), and is the sum of the relative density and relative



dominance (basal area) for a total sum of 200. Dead-standing density (stem/ha) and basal area ( $\text{m}^2/\text{ha}$ ) were also determined. Woody understory composition and density (stems/ha) were determined using nested circular plots 0.0001, 0.001, and 0.01 ha in size located at 15-m intervals along randomly located east-west transects within each study area. Four additional 0.0001-ha circular plots were located 6 m from the center points of each plot center along cardinal compass directions. In the 0.0001-ha plots, woody seedlings ( $\leq 50$  cm tall) were counted; in the 0.001-ha circular plots small saplings ( $> 50$  cm tall and  $< 2.5$  cm dbh) were recorded; and in the 0.01-ha circular plots large saplings (2.5–9.9 cm dbh) were tallied.

**Data Analysis:** The Floristic Quality Index (FQI) was determined for each nature preserve and natural area using the coefficient of conservatism (CC) assigned each species based on a species tolerance to disturbance and its fidelity to habitat integrity (Taft et al. 1997). The FQI, therefore, is a weighted index of species richness ( $N$  = number of species present on a site), and is the arithmetic product of the average coefficient of conservatism ( $C\text{-Value}$  = the average of all species CCs) multiplied by the square root of the native species richness ( $\sqrt{N}$ ) of an inventory site:  $FQI = C\text{-Value} (\sqrt{N})$ . For relatively small areas that are intensively studied, the FQI gives a rapid means of comparison and an indication of the floristic integrity of the site. Using the FQI along with other floristic measures, such as quadrat-based sampling methods, provides a meaningful way of making comparisons among sites. Prairies with an FQI of 35 or higher are usually considered good-quality natural areas (Taft et al. 1997). Though area dependent, the FQI can still be useful in explaining the variation among sites of similar size and habitat (Taft et al. 2006). In our study, the FQI was determined for each of the four natural areas studied, as well as for each of the 15 sand prairie communities surveyed.

The Sorensen Index of Similarity (ISs) was used to determine the degree of vegetation similarity between the prairie areas surveyed throughout the Mississippi River sand deposits (Mueller-Dombois and Ellenberg 1974). In this index [ $ISs = 2C/A+B \times 100$ ],  $A$  equals the number of species in the first community,  $B$  equals the number of species in the second

community, and  $C$  equals the number of species common between the two communities.

Cluster analysis was used to produce a hierarchical classification of sample transects from the sand prairie study sites (PC-ORD; McCune and Mefford 1999) and a variety of distance measures and linkage methods were explored. While there was some variation in the results among methods, cluster analysis using the Euclidean (Pythagorean) distance measure and Ward's linkage method produced a dendrogram similar to Sorensen Distance Measure and Farthest Neighbor Linkage method. This consensus of group clusters was integrated into ordination biplots using both Detrended Correspondence Analysis (DCA) and Principal Components Analysis (PCA). Since all samples (transects) were from a similar vegetation type (dry to dry-mesic sand prairie) and included many shared species, the dataset was amenable to analysis using the linear response model in PCA. Gradient lengths on the first DCA axis (2.5 standard deviations [SD]) were within the range where both linear and Gaussian methods can be effective ordination techniques (Ter Braak and Prentice 1988, Ter Braak 1995). Most plots (i.e., transects [12 of 15]) fall within 2 SD on the first DCA axis indicating most species are responding with little variation over the observed range of environmental conditions. Under these circumstances, a linear response model (e.g., PCA) is appropriate. The graphical depiction of the PCA biplot also was more readily interpretable compared to DCA; consequently, PCA was the preferred ordination technique with this dataset. A correlation matrix was used for the ordination with species scores divided by their standard deviation. The top-ranking 75 species based on importance values were used for the ordination; the remaining 45 species in the dataset all were scarce (present in only one or two transects) and occurred in low percentage cover.

Constrained ordination using community-level parameters as environmental variables (i.e., native species richness, adventive species richness, species density [average species number per quadrat], percent bare ground, mean coefficient of conservatism) with Redundancy Analysis explained 91% of the species-environment relations. However, percent bare ground was the only variable explaining a significant amount of the variation ( $P = 0.01$ ).

## RESULTS

### Lost Mound

A total of 621 species in 353 genera and 108 families was documented (Appendix I). Ferns, fern-allies, and gymnosperms accounted for 21 species in 11 families and 15 genera, while 157 were monocots in 18 families and 75 genera, and 443 were dicots in 79 families and 263 genera. Adventive (exotic) species accounted for 136 taxa, about 22% of all species. Five state-threatened species (Herkert and Ebinger 2002) were recorded: *Besseyia bullii* (kitten tails), *Cyperus grayoides* (sand prairie flat-sedge), *Elymus trachycaulus* (bearded wheat grass), *Equisteum pratense* (meadow horsetail), and *Salvia azurea* (blue sage); and seven state-endangered species were encountered: *Bouteloua gracilis* (blue grama), *Ceanothus herba-ceus* (redroot), *Hudsonia tomentosa* (beach heather), *Mirabilis hirsuta* (hairy umbrella-wort), *Opuntia fragilis* (fragile prickly pear), *Orobanche fasciculata* (clustered broomrape), and *Polanisia jamesii* (James' clammyweed). The FQI was determined only for the dry sand prairie communities at Lost Mound because the FQI is meaningful for only small areas. The FQI for sand prairie communities at this site when adventive species were included was 59.70 with a mean C-value of 2.97, and with the adventive species excluded from the calculations the FQI was 80.00 with a mean C-value of 3.98.

**Blowout Community (early successional dry sand prairie):** Blowouts were numerous at Lost Mound. All had a sparse vegetation cover with relatively few species. In the community surveyed, seven species dominated, all with high mean covers and IVs. Five of these species, *Carex muhlenbergii* (Muhlenberg's sedge), *Dichanthelium villosissimum* (hairy panic grass), *Aristida tuberculosa* (needle grass), *Cyperus schweinitzii* (Schweinitz' sedge), and *Panicum virgatum* (switch grass) were the native graminoid taxa; whereas *Croton glandulosus* (sand croton) and *Ambrosia psilostachya* (western ragweed) were the dominant forbs (Table 1). The 16 remaining species were mostly native dry sand prairie components that were common in surrounding plant communities. The only adventive species, *Mollugo verticillata* (carpetweed) was uncommon with

an IV of 0.8. Bare ground and litter had a mean cover of 63%. This community is the Blowout Formation of Gleason (1910), who describes the four major associations of this formation (windward slope, basin, blowsand, and deposition), and discusses the stages of succession to the bunch-grass association.

**Blowing Sand Community (early successional dry sand prairie):** Areas of blowing sand, generally associated with dune ridges, were common at Lost Mound. These open areas were the result of past disturbances, particularly grazing (Table 1). On the dune ridge *Hudsonia tomentosa* formed extensive low mounds and dominated with a mean cover of 20.4% and an IV of 41.0. *Tephrosia virginiana* (goat's-rue), *Dichanthelium villosissimum*, *Ambrosia psilostachya*, and *Andropogon gerardii* (big bluestem) followed in IV. Most of the other species found in the plots were common sand prairie species. The adventive *Rumex acetosella* (sour dock) was common, ranking eighth in IV, and found in about 50% of the plots. The adventive cool-season *Poa pratensis* (Kentucky blue grass) was present but infrequent. Bare ground and litter had a mean cover of 41%. This community is the *Hudsonia* Association of Gleason (1910), which he commonly found in the Hanover region (Lost Mound).

**Dry Sand Prairie Community (successional with cool season grasses common):** Much of Lost Mound had been subjected to cattle grazing, which kept the vegetation cover sparse and low, and helped decrease the frequency and intensity of "wild" fires. Many of these areas were seeded in cool-season, Eurasian grasses, particularly *Poa pratensis* and *Bromus inermis*. Generally this was done with minimal or no ground preparation. The resulting pastures had a relatively high importance of the cool season grasses, along with a fairly well-developed sand prairie community with most of the prairie grasses and forbs still present (Table 2). In the three areas surveyed, *Poa pratensis* was second in importance on two sites and sixth in importance on the third. On this third site (Primms Prairie), *Bromus inermis* was fifth in importance and the adventive *Rumex acetosella* (sour dock) was second. On all three sites native prairie grasses and forbs were common, with *Poa pratensis*, *Bromus inermis*, and *Rumex acetosella* the chief adventive species encountered.

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Table 1. Frequency (%), mean cover (% of total area) and importance value (I.V.) of the ground layer species encountered in the fall 2005 surveys of a blowout community and a blowing sand community at Lost Mound, Jo Daviess County, Illinois. (\* non-native species)

Species	Blowout Community			Blowing Sand Community		
	Area 1 (n=50)			Area 2 (n=50)		
	Freq.%	Mean Cover	I.V.	Freq.%	Mean Cover	I.V.
<i>Carex muhlenbergii</i>	58	5.96	25.7	48	0.59	6.9
<i>Dichanthelium villosissimum</i>	66	5.57	25.5	66	5.67	17.2
<i>Aristida tuberculosa</i>	94	3.89	24.4	72	1.49	11.3
<i>Cyperus schweinitzii</i>	94	3.51	23.3	54	0.72	8.2
<i>Croton glandulosus</i>	98	2.04	19.5	6	0.08	0.8
<i>Ambrosia psilostachya</i>	78	2.75	19.0	70	2.74	13.1
<i>Panicum virgatum</i>	54	3.63	18.3	22	0.94	4.2
<i>Cyperus lupulinus</i>	60	0.85	10.8	40	0.55	5.9
<i>Tephrosia virginiana</i>	12	2.70	9.7	36	10.92	21.9
<i>Oenothera clelandii</i>	30	0.35	5.1	4	0.02	0.5
<i>Paspalum bushii</i>	12	1.03	4.8	2	0.06	0.3
<i>Polygonella articulata</i>	16	0.42	3.4	32	0.60	4.9
<i>Chamaesyce geyeri</i>	16	0.28	3.0	2	0.01	0.2
<i>Diodia teres</i>	6	0.13	1.2	--	--	--
<i>Leptoloma cognatum</i>	2	0.30	1.2	--	--	--
<i>Carex tosa</i>	6	0.08	1.0	54	2.08	10.3
<i>Koeleria macrantha</i>	4	0.12	1.0	34	1.35	6.4
* <i>Mollugo verticillata</i>	4	0.07	0.8	--	--	--
<i>Coryza canadensis</i>	4	0.02	0.7	--	--	--
<i>Triplasis purpurea</i>	4	0.02	0.7	--	--	--
<i>Asclepias viridiflora</i>	2	0.01	0.3	--	--	--
<i>Monarda punctata</i>	2	0.01	0.3	--	--	--
<i>Sporobolus cryptandrus</i>	2	0.01	0.3	--	--	--
<i>Hudsonia tomentosa</i>	--	--	--	68	20.39	41.0
<i>Andropogon gerardii</i>	--	--	--	36	4.31	11.4
* <i>Rumex acetosella</i>	--	--	--	50	1.62	8.8
<i>Selaginella rupestris</i>	--	--	--	18	2.09	5.5
<i>Cyperus grayoides</i>	--	--	--	24	0.61	4.0
<i>Rhus aromatica</i>	--	--	--	6	2.06	4.0
<i>Schizachyrium scoparium</i>	--	--	--	8	1.41	3.3
<i>Euphorbia corollata</i>	--	--	--	12	0.79	2.8
<i>Lespedeza capitata</i>	--	--	--	14	0.65	2.7
<i>Solidago nemoralis</i>	--	--	--	4	0.31	1.0
* <i>Poa pratensis</i>	--	--	--	6	0.08	0.8
<i>Opuntia macrorhiza</i>	--	--	--	2	0.30	0.7
<i>Plantago patagonica</i>	--	--	--	4	0.02	0.5
<i>Brickellia eupatorioides</i>	--	--	--	2	0.06	0.3
<i>Lithospermum croceum</i>	--	--	--	2	0.06	0.3
<i>Asclepias verticillata</i>	--	--	--	2	0.01	0.2
<i>Aster sericeus</i>	--	--	--	2	0.01	0.2
<i>Bouteloua hirsuta</i>	--	--	--	2	0.01	0.2
<i>Sporobolus clandestinus</i>	--	--	--	2	0.01	0.2
Totals		33.75	200.0		62.62	200.0
Bare ground and litter		63.04			40.60	



tered (Table 2). On these three sites the mean cover of bare ground and litter ranged from 13 to 30%.

**Dry Sand Prairies Community (mid-successional):** On interdunal areas and lower dune slopes, mid-successional dry sand prairies dominated by *Sporobolus clandestinus* (dropseed) and *Selaginella rupestris* (rock spikemoss) were common. These two species combined accounted for over one-third of the importance value. *Sporobolus cryptandrus* (sand dropseed) and *S. compositus* were also present, but in lower numbers. Other common graminoids included *Koeleria macrantha* (June grass), *Leptoloma cognitum* (fall witch grass), *Cyperus lupulinus* (flatsedge), and *C. schweinitzii*; the common forbs were *Ambrosia psilostachya*, *Asclepias verticillata* (horsetail milkweed), and *Opuntia macrorhiza* (plains prickly pear) (Table 3).

On upper dune slopes and dune ridges, another mid-successional dry sand prairie community was sometimes found. *Heterotheca spartea* (porcupine grass), *Opuntia macrorhiza*, and *Selaginella rupestris* dominated the community, and along with the subdominants *Schizachyrium scoparium* (little bluestem) and *Ambrosia psilostachya*, accounted for nearly 60% of the total IV (Table 3). In both of these communities few adventive species other than *Poa pratensis* were encountered. Both communities were heavily grazed in the past and both had a mean cover of bare ground and litter of 22 to 23%.

**Dry Sand Prairie Community (mature or late successional):** Excessive grazing and the introduction of cool season grasses and other exotic species have degraded most of the dry sand prairie community at Lost Mound. Some areas, however, have been fenced and have not recently been subjected to heavy grazing. One area, located on a dune ridge and east-facing dune slope, was fenced in 1995 to exclude grazing. During the spring of 2005 a "wildfire" burned the east-facing slope. This burned area is presently dominated by two native species, *Ambrosia psilostachya* and *Schizachyrium scoparium*, and the adventive *Rumex acetosella* (Table 4). Other common species include the prairie forb *Aster ericoides* (heath aster); two native bunch-grasses, *Koeleria macrantha* and *Leptoloma cognatum*; and the native prairie

shrub *Amorpha canescens* (leadplant). These seven species accounted for more than 50% of the IV. On the unburned dune ridge the dry sand prairie was dominated by *Schizachyrium scoparium* with an IV of 40.4. *Selaginella rupestris*, which was second in IV, formed extensive colonies on the surface of the sand between the other species, while *Ambrosia psilostachya* ranked third with an IV of 20.1. On this prairie the adventive *Rumex acetosella* and *Potentilla recta* (sulfur cinquefoil) ranked fourth and fifth in IV, while native graminoid taxa accounted for the next five species in IV (Table 4). Bare ground and litter had a mean cover of 27% on the unburned, and 38% on the burned part of this prairie. This community is the Mixed Consociates of the Bunch-Grass Association described by Gleason (1910).

**Dry Sand Savanna Community:** Fire suppression, grazing, and other disturbances degraded most of the dry sand savannas at Lost Mound. The savanna surveyed, which had a tree canopy cover of less than 40%, was located in and along the margin of a large stabilized blowout. In parts of this savanna the trees were widely scattered, other areas had nearly 80% closed canopy. *Quercus velutina* (black oak) was the only species present that exceeded 10 cm dbh. This species dominated the seedling and sapling layer and averaged 240 stems/ha ( $\leq 10$  cm dbh.) and 14,323 m<sup>2</sup>/ha of basal area (Table 5). Wind action had exposed the large basal caudex of many of the older black oaks showing that these trees probably originated as grubs. Black oak and species of *Rubus* (dewberries, blackberries, and raspberries), *Rhus* (sumac), and *Prunus* (cherries) were common components of the seedling layer. Saplings averaged fewer than 3,000 stems/ha, nearly all less than 2.5 cm dbh (Table 5).

**Dry Sand Forest Community:** In the southern third of Lost Mound, at the edge of the Mississippi River, is a large stabilized dune covered by dry sand forest. This forest was dominated by *Quercus velutina* with 332 stems/ha, 22,959 m<sup>2</sup>/ha of basal area, and 95% of the IV (Table 6). The only other species reaching tree size ( $\leq 10$  cm dbh) were a few small individuals of *Prunus serotina* (wild black cherry), *Quercus alba* (white oak), *Fraxinus lanceolata* (green ash), and *Juglans nigra* (black walnut). The seedling and small sapling layers were dense.

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Table 2. Frequency (%), mean cover (% of total area), and importance value (I.V.) of the ground layer species encountered in the fall of 2005 in dry sand prairie successional communities dominated by cool season grasses at Lost Mound, Jo Daviess County, Illinois. (\*non-native species)

Species	Schizachyrium/Poa Community Area 3 (n=50)			Tephrosia/Poa Community Area 4 (n=50)			Primms Prairie Area 5 (n=50)		
	Freq. %	Mean Cover	I.V.	Freq. %	Mean Cover	I.V.	Freq. %	Mean Cover	I.V.
<i>Schizachyrium scoparium</i>	100	26.58	45.6	62	10.77	21.8	--	--	--
* <i>Poa pratensis</i>	68	5.63	14.4	76	17.47	32.0	88	7.18	14.3
<i>Ambrosia psilostachya</i>	72	4.98	14.1	16	0.13	2.4	88	12.29	20.1
<i>Selaginella rupestris</i>	46	7.02	14.1	42	9.25	17.1	--	--	--
<i>Opuntia macrorhiza</i>	44	5.19	11.5	2	0.75	1.2	4	0.02	0.3
<i>Koeleria macrantha</i>	50	4.78	11.4	22	1.57	4.9	28	1.36	3.4
<i>Cyperus lupulinus</i>	80	1.15	9.8	20	0.20	2.9	56	0.43	4.4
<i>Asclepias verticillata</i>	60	1.92	8.7	28	0.73	4.8	38	0.24	2.9
<i>Tephrosia virginiana</i>	24	4.68	8.7	94	24.37	42.9	--	--	--
* <i>Rumex acetosella</i>	44	0.96	5.9	--	--	--	94	10.22	18.1
<i>Dichanthelium villosissimum</i>	40	1.03	5.5	46	2.88	10.0	50	2.55	6.4
<i>Helianthus pauciflorus</i>	28	1.31	4.6	--	--	--	--	--	--
<i>Leptoloma cognatum</i>	28	1.07	4.3	10	0.49	2.0	52	2.07	5.9
<i>Rhus aromatica</i>	14	2.13	4.3	4	2.50	3.6	14	1.78	3.0
<i>Carex tonsa</i>	34	0.42	4.1	12	0.11	1.7	--	--	--
<i>Aster sericeus</i>	12	1.48	3.2	--	--	--	--	--	--
<i>Cyperus schweinitzii</i>	24	0.37	3.0	2	0.01	0.3	12	0.06	0.9
<i>Physalis virginiana</i>	22	0.51	3.0	54	2.03	10.0	30	0.55	2.7
<i>Polygala polygama</i>	20	0.25	2.4	--	--	--	8	0.04	0.6
<i>Plantago patagonica</i>	20	0.15	2.3	6	0.03	0.8	12	0.06	0.9
<i>Panicum virgatum</i>	10	0.73	2.0	14	0.12	2.0	86	8.03	15.1
<i>Dichanthelium oligosanthes</i>	14	0.32	1.9	--	--	--	42	1.54	4.7
<i>Carex muhlenbergii</i>	14	0.22	1.8	22	0.41	3.5	24	0.21	2.5
<i>Andropogon gerardii</i>	2	0.75	1.2	--	--	--	--	--	--
<i>Conyza canadensis</i>	10	0.15	1.2	--	--	--	50	1.28	5.0
<i>Euphorbia corollata</i>	8	0.33	1.2	--	--	--	--	--	--
<i>Equisetum laevigatum</i>	10	0.05	1.1	--	--	--	30	0.15	2.3
<i>Lithospermum croceum</i>	6	0.32	1.0	--	--	--	84	9.22	16.3
<i>Pseudognaphalium obtusifolium</i>	6	0.32	1.0	--	--	--	--	--	--
* <i>Achillea millefolium</i>	8	0.04	0.9	--	--	--	44	0.81	3.9
<i>Lespedeza capitata</i>	8	0.09	0.9	--	--	--	44	2.41	5.7
<i>Dichanthelium perlongum</i>	6	0.18	0.8	4	0.12	0.7	--	--	--
<i>Paspalum bushii</i>	6	0.08	0.7	--	--	--	78	5.84	12.0
<i>Brickellia eupatorioides</i>	4	0.12	0.6	--	--	--	52	3.23	7.3
<i>Erigeron strigosus</i>	4	0.07	0.5	--	--	--	--	--	--
<i>Oxalis stricta</i>	4	0.07	0.5	--	--	--	20	0.10	1.5
* <i>Kummerowia stipulacea</i>	4	0.02	0.4	--	--	--	--	--	--
<i>Polygonum tenue</i>	4	0.02	0.4	--	--	--	--	--	--
<i>Callirhoe triangulata</i>	2	0.06	0.3	--	--	--	--	--	--
<i>Eragrostis spectabilis</i>	2	0.06	0.3	2	0.06	0.4	2	0.06	0.2
<i>Oenothera clelandii</i>	2	0.01	0.2	--	--	--	4	0.07	0.4
<i>Sporobolus cryptandrus</i>	2	0.01	0.2	--	--	--	22	0.21	1.7
<i>Opuntia fragilis</i>	--	--	--	88	4.44	17.8	--	--	--
<i>Solanum carolinense</i>	--	--	--	28	1.75	6.1	16	0.28	1.6
<i>Heterostipa spartea</i>	--	--	--	14	0.27	2.2	8	0.09	0.7
<i>Viola pedata</i>	--	--	--	12	0.21	1.9	--	--	--
<i>Bouteloua hirsuta</i>	--	--	--	12	0.16	1.8	--	--	--
<i>Croton glandulosus</i>	--	--	--	6	0.37	1.4	38	0.24	2.9
<i>Triplasis purpurea</i>	--	--	--	4	0.12	1.2	--	--	--
<i>Tradescantia ohimensis</i>	--	--	--	6	0.08	0.9	--	--	--
<i>Sporobolus clandestinus</i>	--	--	--	4	0.02	0.6	4	0.31	0.7
<i>Aristida tuberculosa</i>	--	--	--	2	0.06	0.4	--	--	--
* <i>Mollugo verticillata</i>	--	--	--	2	0.06	0.4	--	--	--

Table 2 cont Species	Schizachyrium/Poa Community Area 3 (n=50)			Tephrosia/Poa Community Area 4 (n=50)			Primms Prairie Area 5 (n=50)		
	Freq. %	Mean Cover	I.V.	Freq. %	Mean Cover	I.V.	Freq. %	Mean Cover	I.V.
<i>Chamaesce geyeri</i>	--	--	--	2	0.01	0.3	--	--	--
* <i>Bromus inermis</i>	--	--	--	--	--	--	50	9.84	14.7
<i>Verbena stricta</i>	--	--	--	--	--	--	28	1.26	3.3
<i>Sorghastrum nutans</i>	--	--	--	--	--	--	14	1.83	3.1
<i>Monarda punctata</i>	--	--	--	--	--	--	26	0.43	2.3
<i>Poinsettia dentata</i>	--	--	--	--	--	--	18	0.14	1.4
* <i>Potentilla recta</i>	--	--	--	--	--	--	14	0.27	1.3
<i>Strophostyles helvula</i>	--	--	--	--	--	--	10	0.15	0.9
<i>Gleditsia triacanthos</i>	--	--	--	--	--	--	8	0.14	0.8
<i>Chamaecrista fasciculata</i>	--	--	--	--	--	--	8	0.04	0.6
<i>Crotalaria sagittalis</i>	--	--	--	--	--	--	6	0.08	0.5
<i>Rosa carolina</i>	--	--	--	--	--	--	2	0.30	0.4
* <i>Saponaria officinalis</i>	--	--	--	--	--	--	4	0.07	0.4
<i>Senecio plattensis</i>	--	--	--	--	--	--	4	0.12	0.4
<i>Physalis heterophylla</i>	--	--	--	--	--	--	4	0.02	0.3
<i>Physalis subglabrata</i>	--	--	--	--	--	--	4	0.02	0.3
<i>Asclepias syriaca</i>	--	--	--	--	--	--	2	0.06	0.2
<i>Juniperus virginiana</i>	--	--	--	--	--	--	2	0.06	0.2
<i>Prunus serotina</i>	--	--	--	--	--	--	2	0.06	0.2
<i>Cirsium discolor</i>	--	--	--	--	--	--	2	0.01	0.1
<i>Phyla lanceolata</i>	--	--	--	--	--	--	2	0.01	0.1
* <i>Potentilla argentea</i>	--	--	--	--	--	--	2	0.01	0.1
Totals		75.63	200.0		81.55	200.0		87.85	200.0
Bare ground and litter		30.36			16.82			13.08	

Woody seedlings averaged 34,066 stems/ha, small saplings averaged 10,533 stems/ha, but large saplings averaged only 468 stems/ha (Table 6). *Rubus allegheniensis* (common blackberry) dominated the seedling and small sapling layer with 17,188 and 2,813 stems/ha, respectively. Seedlings and small saplings of *Cornus racemosa* (gray dogwood) and *Prunus virginiana* (common chokecherry) were also common (Table 6).

**Dry-Mesic Sand Forest Community:** Along the northern edge of Lost Mound is a relatively extensive upland sand forest, most of which has been degraded by fire suppression, exotic species invasion, lumbering, and other human activities. Small mature second-growth forest inclusions of a few ha are occasional in this area. *Quercus alba* and *Q. velutina* were the dominant species, and together accounted for 69% of the IV, averaged 177 stems/ha, and had a combined basal area of 23,438 m<sup>2</sup>/ha (Table 7). Twelve other species reached tree size ( $\leq 10$  cm dbh) with *Carya cordiformis* (bitternut hickory) and *Prunus serotina* the

most important. Woody seedlings were abundant with 30,158 stems/ha. *Quercus alba* and *Prunus serotina* seedlings were the most common, but seedlings of many species of shrubs were also present. Small and large saplings were not abundant, resulting in an open understory (Table 7).

**Wet-mesic Floodplain Forest Community:** In the floodplain area immediately south of Lock and Dam 12, the hydrology influencing the floodplain forest and backwater sloughs has been altered since the dam was completed in 1939. Extensive wet-mesic floodplain forests grow on the exposed floodplains. *Acer saccharinum* (silver maple) dominated and accounted for 91% of the IV (182.9) with 217 stems/ha and a basal area of 34,175 m<sup>2</sup>/ha. Small numbers of *Ulmus americana* (American elm), *Fraxinus lanceolata*, and *Celtis occidentalis* (hackberry), were encountered (Table 8). Woody seedlings were common, but few would enter the sapling layer as indicated by the small number of saplings present.

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Table 3. Frequency (%), mean cover (% of total area), and importance value (I.V.) of the ground layer species encountered in the fall of 2005 in dry sand prairie mid-successional communities at Lost Mound, Jo Daviess County, Illinois. (\*non-native species)

Species	Sporobolus/Selaginella Community Area 6 (n=50)			Heterostipa/Opuntia Community Area 7 (n=50)		
	Freq.%	Mean Cover	I.V.	Freq.%	Mean Cover	I.V.
<i>Sporobolus clandestinus</i>	100	28.20	46.1	--	--	--
<i>Selaginella rupestris</i>	68	12.37	22.4	66	15.36	25.1
<i>Koeleria macrantha</i>	86	8.16	18.3	32	2.36	6.3
<i>Ambrosia psilostachya</i>	98	6.97	17.9	84	7.31	17.8
<i>Asclepias verticillata</i>	96	5.06	15.3	28	0.63	3.9
<i>Cyperus lupulinus</i>	92	0.66	9.1	76	1.66	10.5
<i>Opuntia macrorhiza</i>	52	3.08	8.8	80	16.53	28.0
<i>Leptoloma cognatum</i>	56	1.76	7.3	22	1.18	3.9
<i>Cyperus schweinitzii</i>	66	0.82	7.0	16	0.28	2.1
<i>Sporobolus cryptandrus</i>	54	1.10	6.3	8	0.04	1.0
<i>Plantago patagonica</i>	62	0.31	6.0	10	0.05	1.2
* <i>Poa pratensis</i>	56	0.48	5.6	26	1.15	4.2
<i>Physalis virginiana</i>	36	0.87	4.3	12	0.40	1.8
<i>Dichanthelium villosissimum</i>	24	0.37	2.7	38	0.78	5.2
<i>Monarda punctata</i>	12	1.03	2.5	--	--	--
<i>Dichanthelium oligosanthes</i>	20	0.30	2.2	2	0.01	0.2
<i>Lithospermum croceum</i>	18	0.43	2.2	12	0.21	1.5
<i>Oenothera clelandii</i>	22	0.16	2.2	--	--	--
<i>Rhus aromatica</i>	2	1.25	1.9	--	--	--
* <i>Achillea millefolium</i>	10	0.44	1.5	--	--	--
<i>Panicum virgatum</i>	12	0.16	1.3	20	0.30	2.6
<i>Schizachyrium scoparium</i>	4	0.60	1.2	82	8.68	19.2
<i>Paspalum setaceum</i>	10	0.10	1.0	--	--	--
<i>Solidago nemoralis</i>	6	0.37	1.0	--	--	--
<i>Carex mühlenbergii</i>	8	0.04	0.8	22	0.41	3.0
<i>Lespedeza capitata</i>	8	0.04	0.8	--	--	--
* <i>Potentilla recta</i>	6	0.08	0.6	--	--	--
<i>Sorghastrum nutans</i>	6	0.08	0.6	--	--	--
<i>Verbena stricta</i>	4	0.12	0.6	--	--	--
<i>Eragrostis spectabilis</i>	4	0.07	0.5	--	--	--
<i>Penstemon pallidus</i>	4	0.02	0.4	--	--	--
<i>Physalis heterophylla</i>	2	0.06	0.3	--	--	--
<i>Sporobolus compositus</i>	2	0.06	0.3	--	--	--
<i>Antennaria neglecta</i>	2	0.01	0.2	--	--	--
<i>Aristida basiramea</i>	2	0.01	0.2	--	--	--
<i>Bouteloua hirsuta</i>	2	0.01	0.2	12	0.45	1.8
<i>Oxalis stricta</i>	2	0.01	0.2	--	--	--
<i>Pseudognaphalium obtusifolium</i>	2	0.01	0.2	--	--	--
<i>Heterostipa spartea</i>	--	--	--	98	16.72	30.3
<i>Tephrosia virginiana</i>	--	--	--	28	5.52	9.6
<i>Carex tomsa</i>	--	--	--	24	0.17	2.9
<i>Equisetum laevigatum</i>	--	--	--	24	0.12	2.8
<i>Brickellia eupatorioides</i>	--	--	--	12	0.98	2.4
<i>Callirhoe triangulata</i>	--	--	--	4	1.55	2.3
<i>Andropogon gerardii</i>	--	--	--	8	0.96	2.0
<i>Ceanothus herbaceus</i>	--	--	--	4	1.26	2.0
<i>Croton glandulosus</i>	--	--	--	10	0.79	2.0
<i>Euphorbia corollata</i>	--	--	--	10	0.39	1.5
<i>Helianthus pauciflorus</i>	--	--	--	6	0.18	0.9
<i>Paspalum bushii</i>	--	--	--	4	0.36	0.9
<i>Chrysopsis camporum</i>	--	--	--	6	0.03	0.7
* <i>Chenopodium album</i>	--	--	--	2	0.01	0.2
<i>Solanum carolinense</i>	--	--	--	2	0.01	0.2
Totals		75.67	200.0		86.84	200.0
Bare ground and litter		22.36			22.99	

Table 4. Frequency (%), mean cover (% of total area), and importance value (I.V.) of the ground layer species encountered in the fall of 2005 in burned and unburned mature dry sand prairie communities at Lost Mound, Jo Daviess County, Illinois. (\*non-native species)

Species	Unburned Dry Sand Prairie Community Area 8 (n=50)			Burned Dry Sand Prairie Community Area 9 (n=50)		
	Freq.%	Mean Cover	I.V.	Freq.%	Mean Cover	I.V.
<i>Schizachyrium scoparium</i>	96	21.30	40.4	90	5.42	16.2
<i>Selaginella rupestris</i>	78	10.94	23.2	24	0.56	2.9
<i>Ambrosia psilostachya</i>	86	8.43	20.1	88	9.56	22.7
* <i>Rumex acetosella</i>	78	1.58	9.1	98	8.85	22.5
* <i>Potentilla recta</i>	70	1.92	9.0	30	1.47	4.9
<i>Andropogon gerardii</i>	22	4.59	8.8	14	2.07	4.5
<i>Cyperus lupulinus</i>	80	1.15	8.6	60	0.55	5.8
<i>Koeleria macrantha</i>	64	1.60	7.9	66	2.83	10.0
<i>Carex tonsa</i>	62	0.86	6.7	42	0.31	4.0
<i>Leptoloma cognatum</i>	50	1.52	6.6	54	3.34	9.8
* <i>Poa pratensis</i>	46	1.69	6.6	24	0.41	2.7
<i>Opuntia macrorhiza</i>	26	2.81	6.4	34	3.19	8.0
<i>Sorghastrum nutans</i>	22	1.63	4.4	14	0.27	1.5
<i>Dichanthelium villosissimum</i>	36	0.77	4.3	46	0.38	4.4
* <i>Achillea millefolium</i>	36	0.38	3.7	46	0.68	4.9
<i>Carex muhlenbergii</i>	36	0.28	3.5	14	0.07	1.2
<i>Asclepias verticillata</i>	36	0.18	3.4	68	0.49	6.4
<i>Bouteloua hirsuta</i>	18	1.11	3.3	4	0.07	0.4
<i>Physalis virginiana</i>	28	0.54	3.2	24	0.27	2.4
<i>Solidago nemoralis</i>	16	0.81	2.6	18	0.97	3.0
<i>Lithospermum croceum</i>	20	0.40	2.3	14	1.38	3.3
<i>Polygala polygama</i>	22	0.11	2.1	28	0.24	2.7
<i>Dichanthelium oligosanthes</i>	20	0.20	2.0	8	0.04	0.8
<i>Plantago patagonica</i>	20	0.10	1.9	--	--	--
<i>Monarda punctata</i>	12	0.45	1.7	2	0.06	0.3
<i>Oenothera clelandii</i>	14	0.12	1.4	16	0.18	1.6
<i>Aster ericoides</i>	8	0.19	1.0	60	4.33	11.9
<i>Sporobolus cryptandrus</i>	10	0.05	1.0	--	--	--
<i>Rhus aromatica</i>	2	0.30	0.7	12	1.93	4.1
<i>Conyza canadensis</i>	6	0.03	0.5	--	--	--
<i>Aristida basiramea</i>	4	0.02	0.3	--	--	--
<i>Aristida tuberculosa</i>	4	0.02	0.3	--	--	--
<i>Cyperus schweinitzii</i>	4	0.02	0.3	18	0.09	1.5
<i>Helianthemum canadense</i>	2	0.06	0.3	--	--	--
<i>Panicum virgatum</i>	4	0.02	0.3	--	--	--
* <i>Potentilla argentea</i>	2	0.06	0.3	--	--	--
<i>Croton glandulosus</i>	2	0.01	0.2	2	0.01	0.2
<i>Dichanthelium perlongum</i>	2	0.01	0.2	2	0.01	0.2
<i>Draba reptans</i>	2	0.01	0.2	--	--	--
<i>Gleditsia triacanthos</i>	2	0.01	0.2	--	--	--
<i>Hieracium longipilum</i>	2	0.01	0.2	--	--	--
<i>Liatris aspera</i>	2	0.01	0.2	--	--	--
<i>Linum sulcatum</i>	2	0.01	0.2	2	0.01	0.2
<i>Oxalis stricta</i>	2	0.01	0.2	30	0.35	3.1
* <i>Poa compressa</i>	2	0.01	0.2	--	--	--
<i>Amorpha canescens</i>	--	--	--	46	2.96	8.6
<i>Tephrosia virginiana</i>	--	--	--	16	2.16	4.8
<i>Ionactis linariifolius</i>	--	--	--	18	1.90	4.5
<i>Helianthus occidentalis</i>	--	--	--	18	1.16	3.3
<i>Coreopsis palmata</i>	--	--	--	8	0.72	1.9
<i>Aster sericeus</i>	--	--	--	8	0.67	1.8
<i>Anemone cylindrica</i>	--	--	--	8	0.38	1.3
<i>Callirhoe triangulata</i>	--	--	--	6	0.42	1.2
<i>Eragrostis spectabilis</i>	--	--	--	10	0.20	1.1
<i>Ceanothus americanus</i>	--	--	--	2	0.30	0.7
<i>Heterostipa spartea</i>	--	--	--	6	0.13	0.7
<i>Physalis subglabrata</i>	--	--	--	4	0.12	0.5
<i>Bouteloua curtipendula</i>	--	--	--	2	0.06	0.3
<i>Equisetum laevigatum</i>	--	--	--	2	0.06	0.3
<i>Froelichia gracilis</i>	--	--	--	4	0.02	0.3
<i>Asclepias viridiflora</i>	--	--	--	2	0.01	0.2
<i>Dalea purpurea</i>	--	--	--	2	0.01	0.2
<i>Solanum carolinense</i>	--	--	--	2	0.01	0.2
Totals		66.33	200.0		61.68	200.0
Bare ground and litter		26.70			38.10	

Table 5. Size class density (#/ha), basal area (m<sup>2</sup>/ha), relative values, importance value (I.V.), and average diameter (cm) of the woody species encountered in 2005 in a dry sand savanna associated with a blowout at Lost Mound, Jo Daviess County, Illinois. (\*non-native species)

Species	Seed-lings	Small Sap-lings	Large Sap-lings	Trees (#/ha)	Basal Area (m <sup>2</sup> /ha)	Rel. Den.	Rel. Dom.	I. V.	Av. Diam. (cm)
<i>Quercus velutina</i>	4583	1167	167	240	14.323	100.0	100.0	200.0	24.2
<i>Rubus flagellaris</i>	3750	--	--	--	--	--	--	--	--
<i>Rhus aromatica</i>	2917	--	--	--	--	--	--	--	--
<i>Prunus virginiana</i>	1667	583	--	--	--	--	--	--	--
<i>Prunus serotina</i>	1250	375	17	--	--	--	--	--	--
<i>Juniperus virginiana</i>	833	167	50	--	--	--	--	--	--
<i>Rubus occidentalis</i>	417	--	--	--	--	--	--	--	--
<i>Ribes missouriense</i>	--	292	--	--	--	--	--	--	--
<i>Rubus allegheniensis</i>	--	42	--	--	--	--	--	--	--
* <i>Rosa multiflora</i>	--	42	--	--	--	--	--	--	--
<i>Carya ovata</i>	--	--	17	--	--	--	--	--	--
Totals	15417	2668	251	240	14.323	100.0	100.0	200.0	

Ayers Sand Prairie Nature Preserve

A total of 175 species in 132 genera and 56 families was documented (Appendix I). Ferns, ferns-allies, and gymnosperms accounted for 4 species, while 42 were monocots in 4 families and 28 genera, and 129 were dicots in 48 families and 100 genera. Adventive species accounted for 36 taxa, about 20% of all species. The state-threatened (Herkert and Ebinger 2002) *Cyperus grayoides* was a common associate of blowouts. The FQI for this site when adventive species were included was 47.62 with a mean C-value of 3.60, and with the adventive species excluded from the calculations the FQI was 52.73 with a mean C-value of 4.41.

**Blowing Sand Community (early successional):** In areas of blowing sand, plants were widely scattered and bare ground and litter averaged 61% cover. Numerous species were established in these areas with *Aristida tuberculosa* (IV of 32.1), *Dichanthelium villosissimum* (IV of 27.3) and *Ambrosia psilostachya* (IV of 17.9) the most common. Most of the species associated with the mature and disturbed dry sand prairie were also found, but in low numbers (Table 9). A few species, such as *Carex tonsa* (shaved sedge), *Callirhoe triangulata* (poppy mallow), *Viola pedata* (bird's-foot violet), *Cyperus schweinitzii*, *Liatris aspera* (rough blazing-star), *Polygonella articulata* (jointweed), and *Chamaesyce geyeri* (Geyer's spurge) were more common in these areas of blowing sand

than in the mature or disturbed sand prairies (Table 9).

**Dry Sand Prairie Community (mid-successional):** The disturbed dry sand prairie community had a high species diversity that included many taxa associated with dry sand prairies. Two bunch-grasses, *Dichanthelium villosissimum* and *Koeleria macrantha*, dominated this community with IVs of 37.0 and 30.1, respectively (Table 9). The disturbance species *Croton glandulosus* (IV of 15.5) and *Aristida tuberculosa* (IV of 13.2) were third and forth in IV, followed by *Ambrosia psilostachya* and *Hudsonia tomentosa*. Bare ground and litter averaged 46% cover.

**Dry Sand Prairie Community (mature or late successional):** In the mature dry sand prairie *Schizachyrium scoparium* dominated with an IV of 52.5 and a mean cover of 31.4 (Table 9). *Ambrosia psilostachya* was second with an IV of 26.4, followed by *Solidago nemoralis* (IV of 14.1), and *Koeleria macrantha* (IV of 13.0). The remaining 40 species encountered in the plots mostly had low frequencies and mean covers. The grasses formed extensive clumps while most other species grew in spaces between clumps, and were referred to as interstitial species by Gleason (1910). The exotic species *Achillea millefolium*, *Mollugo verticillata*, and *Poa pratensis* were rare. Bare ground and litter averaged 28% cover (Table 9).



Table 6. Size class density (#/ha), basal area (m<sup>2</sup>/ha), relative values, importance value (I.V.), and average diameter (cm) of the woody species encountered in 2005 in a mature second growth dry upland sand forest community associated with dune topography at Lost Mound, Jo Daviess County, Illinois. (\*non-native species)

Species	Seed-lings	Small Sap-lings	Large Sap-lings	Trees (#/ha)	Basal Area (m <sup>2</sup> /ha)	Rel. Den.	Rel. Dom.	I. V.	Av. Diam. (cm)
<i>Quercus velutina</i>	3125	125	31	332	22.599	92.2	98.4	190.6	26.9
<i>Prunus serotina</i>	1094	750	356	24	0.310	6.6	1.4	8.0	12.7
<i>Quercus alba</i>	--	--	--	2	0.025	0.6	0.1	0.7	12.6
<i>Fraxinus lanceolata</i>	313	188	13	1	0.015	0.3	0.1	0.4	13.7
<i>Juglans nigra</i>	--	--	--	1	0.010	0.3	--	0.3	11.4
<i>Rubus allegheniensis</i>	17188	2813	--	--	--	--	--	--	--
<i>Cornus racemosa</i>	4688	1844	6	--	--	--	--	--	--
<i>Prunus virginiana</i>	1875	2688	6	--	--	--	--	--	--
<i>Zanthoxylum americanum</i>	1406	344	--	--	--	--	--	--	--
<i>Rubus occidentalis</i>	1250	812	--	--	--	--	--	--	--
<i>Ribes missouriense</i>	1094	406	--	--	--	--	--	--	--
<i>Gleditsia triacanthos</i>	938	125	6	--	--	--	--	--	--
<i>Carya cordiformis</i>	313	94	31	--	--	--	--	--	--
<i>Celtis occidentalis</i>	313	188	13	--	--	--	--	--	--
<i>Rhus aromatica</i>	313	--	--	--	--	--	--	--	--
* <i>Rosa multiflora</i>	156	--	--	--	--	--	--	--	--
<i>Juniperus virginiana</i>	--	94	--	--	--	--	--	--	--
<i>Malus ioensis</i>	--	31	--	--	--	--	--	--	--
<i>Ulmus americana</i>	--	31	6	--	--	--	--	--	--
Totals	34066	10533	468	360	22.959	100.0	100.0	200.0	--

Table 7. Size class density (#/ha), basal area (m<sup>2</sup>/ha), relative values, importance value (I.V.), and average diameter (cm) of the woody species encountered in 2005 in a mature second growth dry-mesic upland sand forest at Lost Mound, Jo Daviess County, Illinois. (\*non-native species)

Species	Seed-lings	Small Sap-lings	Large Sap-lings	Trees (#/ha)	Basal Area (m <sup>2</sup> /ha)	Rel. Den.	Rel. Dom.	I. V.	Av. Diam. (cm)
<i>Quercus alba</i>	6563	47	188	99	14.086	28.3	52.6	80.9	40.0
<i>Quercus velutina</i>	1719	16	--	78	9.352	22.3	34.9	57.2	37.7
<i>Carya cordiformis</i>	1719	188	331	63	.964	18.0	3.6	21.6	13.4
<i>Prunus serotina</i>	4531	--	38	38	.689	10.9	2.6	13.5	14.5
<i>Ulmus americana</i>	1875	16	94	20	.448	5.7	1.7	7.4	16.0
<i>Ulmus rubra</i>	2500	--	63	15	.308	4.2	1.2	5.4	15.7
<i>Celtis occidentalis</i>	2344	109	63	11	.275	3.1	1.0	4.1	17.0
* <i>Robinia pseudoacacia</i>	156	--	38	10	.107	2.8	0.4	3.2	11.7
<i>Tilia americana</i>	--	--	--	7	.150	2.0	0.6	2.6	16.3
<i>Quercus rubra</i>	--	--	--	3	.217	0.9	0.8	1.7	26.1
<i>Betula nigra</i>	--	--	--	3	.054	0.9	0.2	1.1	14.8
<i>Carya ovata</i>	--	--	--	1	.069	0.3	0.2	0.5	29.6
<i>Juglans cinerea</i>	--	--	--	1	.015	0.3	0.1	0.4	13.6
* <i>Morus alba</i>	--	--	--	1	.025	0.3	0.1	0.4	18.0
<i>Rubus allegheniensis</i>	4063	359	--	--	--	--	--	--	--
<i>Ribes missouriense</i>	1719	47	--	--	--	--	--	--	--
<i>Gleditsia triacanthos</i>	781	--	--	--	--	--	--	--	--
<i>Zanthoxylum americanum</i>	625	47	--	--	--	--	--	--	--
<i>Cornus racemosa</i>	469	313	13	--	--	--	--	--	--
<i>Rubus occidentalis</i>	469	94	--	--	--	--	--	--	--
<i>Juniperus virginiana</i>	313	--	--	--	--	--	--	--	--
<i>Celastrus scandens</i>	156	--	--	--	--	--	--	--	--
* <i>Lonicera tatarica</i>	156	--	--	--	--	--	--	--	--
<i>Corylus americana</i>	--	16	--	--	--	--	--	--	--
* <i>Rosa multiflora</i>	--	47	--	--	--	--	--	--	--
<i>Acer negundo</i>	--	--	6	--	--	--	--	--	--
Totals	30158	1299	834	350	26.759	100.0	100.0	--	--

## Thompson-Fulton Sand Prairie Nature Preserve

A total of 182 species in 133 genera and 54 families was documented (Appendix I). Ferns, fern-allies, and gymnosperms accounted for 5 species, while 42 were monocots in 4 families and 28 genera, and 135 were dicots in 46 families and 101 genera. Adventive species accounted for 38 taxa, about 20% of all species. The state-endangered (Herkert and Ebinger 2002) *Penstemon grandiflorus* (large-flowered beardtongue) was relatively common in a small part of the preserve, while the state-threatened *Cyperus grayoides* was occasionally encountered. The FQI for this site when adventive species were included was 46.81 with a mean C-value of 3.47, and with the adventive species excluded from the calculations the FQI was 52.86 with a mean C-value of 4.42.

**Dry Sand Prairie Community (early successional):** The disturbance community contained many species commonly encountered in dry sand prairies. The most important forbs of this community were *Opuntia macrorhiza* (IV of 31.6) and *Ambrosia psilostachya* (IV of 24.8). The important grasses included the two bunch-grasses *Koeleria macrantha* (IV of 21.2) and *Dichanthelium villosissimum* (IV of 12.7) along with the common disturbance area grass *Aristida tuberculosa* (IV of 23.6) (Table 10). *Schizachyrium scoparium* was scarce; only a few scattered individuals were observed and none of these were found in plots. Three adventive species (*Rumex acetosella*, *Mollugo verticillata*, *Bromus tectorum*) were encountered in the plots, all with IV's of 1.7 or lower. Bare ground and litter mean cover was 7% (Table 10).

**Dry Sand Prairie Community (mature or late successional):** *Schizachyrium scoparium*, the leading dominant of the mature sand prairie, had an IV of 39.4 and a mean cover of 20.9% (Table 10). *Opuntia macrorhiza* was second with an IV of 31.7, followed by *Ambrosia psilostachya* (IV of 26.4), *Tephrosia virginiana* (IV of 21.9), and *Dichanthelium villosissimum* (IV of 21.8). Except for *Tephrosia virginiana*, which generally had a clumped distribution, these five species had frequencies of 84–91% with a mean cover higher than 8.0% (Table 10). *Schizachyrium scoparium* and *D. villosissimum*

grew in clumps 10–40 cm across, forming the bunch-grass association described by Gleason (1910). Most other species grew in spaces between clumps. Of the remaining 24 species encountered in the plots, most had frequencies of less than 50% and IV's lower than 8.0. The exotic species *Rumex acetosella* was rare, while bare ground and litter mean cover was 22% (Table 10).

## Big River State Forest

A total of 162 species in 127 genera and 54 families was documented (Appendix I). Gymnosperms accounted for 2 species, while 41 were monocots in 5 families and 27 genera, and 162 were dicots in 54 families and 127 genera. Adventive species accounted for 37 taxa, about 20% of all species. The state-endangered (Herkert and Ebinger 2002) *Penstemon grandiflorus* and *Stylisma pickeringii* (Patterson bindweed) were encountered in the dry sand prairie. The FQI for this site when adventive species were included was 38.18 with a mean C-value of 3.00, and with the adventive species excluded from the calculations the FQI was 43.47 with a mean C-value of 3.89.

**Dry Sand Prairie Community (mature or late successional):** The leading dominant of the mature sand prairie was *Schizachyrium scoparium* with an IV of 41.9 and a mean cover of 34% (Table 11). This species formed extensive clumps, many more than 40 cm across, while most other taxa were interstitial species. *Solidago nemoralis* (gray goldenrod) was second with an IV of 24.3, followed by *Opuntia macrorhiza* (IV of 19.0), and *Ambrosia psilostachya* (IV of 18.4). *Lespedeza capitata* (round-headed bush clover), *Stylisma pickeringii*, and *Monarda punctata* (horsemint) had IV's exceeding 10, while *Dichanthelium villosissimum*, *Cyperus lupulinus*, and *Commelina erecta* (day flower) had frequencies greater than 75% (Table 11). Most of the remaining species encountered had frequencies of less than 50% and IV's lower than 5.0. The only exotic species in the plots, *Poa pratensis* and *Chenopodium album*, were rare, having an IV of 0.2. Bare ground and litter had a mean cover of 10.7%, though in some areas the herbaceous vine, *Stylisma pickeringii* completely covered the plots (Table 11).

Table 8. Size class density (#/ha), basal area (m<sup>2</sup>/ha), relative values, importance value (I.V.), and average diameter (cm) of the woody species encountered in 2005 in a wet-mesic floodplain forest at the edge of the Mississippi River, Lost Mound, Jo Daviess County, Illinois. (\*non-native species)

Species	Seed- lings	Small Sap- lings	Large Sap- lings	Trees (#/ha)	Basal Area (m <sup>2</sup> / ha)	Rel. Den.	Rel. Dom.	I. V.	Av. Diam. (cm)
<i>Acer saccharinum</i>	80938	--	6	217	34.175	87.9	95.0	182.9	41.7
<i>Ulmus americana</i>	21563	344	--	25	1.151	10.1	3.2	13.3	23.5
<i>Fraxinus lanceolata</i>	7813	156	--	4	0.596	1.6	1.7	3.3	23.5
<i>Celtis occidentalis</i>	--	--	--	1	0.026	0.4	0.1	0.5	18.2
* <i>Morus alba</i>	156	--	--	--	--	--	--	--	--
Totals	110470	500	6	247	35.948	100.0	100.0	200.0	--

Dry Sand Savanna Community (degraded):

Dry sand forest occurs just to the north of the dry sand prairie and continues for more than 1 km. Probably clear-cut soon after settlement, this forest has also been subjected to more recent cutting and fire suppression. *Quercus velutina* and *Q. marilandica* (blackjack oak) dominated this degraded sand savanna, which, due to fire suppression, is now a closed canopy forest. On the site trees averaged 588 stems/ha with an average basal area of 17.324 m<sup>2</sup>/ha (Table 12). The oaks averaged 17.3 to 18.7 cm dbh, and except for a few *Juniperus virginiana* (red cedar) and *Prunus serotina*, were the only species that reached tree size (≥10 cm dbh). The seedling and sapling layers were dense; woody seedlings averaged 19,376 stems/ha, small saplings averaged 11,187 stems/ha, but large saplings averaged only 318 stems/ha (Table 12). Black oak dominated the seedling layer (7,500 stems/ha) and was second in small saplings (1,594 stems/ha) and large saplings (106 stems/ha). Blackjack oak was first in large saplings with 131 stems/ha. Species of *Rubus* (blackberries and raspberries) and *Cornus drummondii* (rough-leaved dogwood) were very common components of the seedling and small sapling layers.

DATA ANALYSIS AND SITE SIMILARITY

A summary of the floristic data and the Floristic Quality Index for each of the 15 prairie study sites (9 transects at Lost Mound, 3 at Ayers Nature Preserve, 2 at Thomson-Fulton Nature Preserve, and 1 at Big River State Forest) are

included in Table 13. In this table the 15 study sites are grouped by the amount of past and present disturbances and the extent to which *Schizachyrium scoparium* dominated each community. Throughout the dry sand prairies of the Mississippi River valley in northwestern Illinois, *Schizachyrium scoparium* is usually one of the dominant species, although its importance decreased in successional and disturbance communities. Among all sites, native species richness ranged from 22 to 46 while adventive species richness was low, ranging from 1 to 7 species; the percent of native taxa exceeded 90% at all but two sites (Table 13). Little variation occurs in the Floristic Quality Index (FQI) of the sites (Table 13). The FQI for the sites ranged from 20.74 to 35.07, with only two exceeding 30.

Within the Mississippi River sand deposits, many of the sand prairie communities studied had a relatively high degree of similarity (Table 14). The Sorensen Indices of Similarity (ISs) for the 15 sand prairie areas examined ranged from 35.6% to 83.9% with most values above 50%. The lowest ISs was between the blowout community (Area 1) and the burned dry sand prairie (Area 9), both at Lost Mound. The highest ISs was between the blowing sand community at Ayers Nature Preserve (Area 12) and the successional dry sand prairie at Thomson-Fulton Nature Preserve (Area 14). All communities at Ayers Nature Preserve and Thomson-Fulton Nature Preserve were very similar as shown by the constantly high ISs, which ranged from 59.3 to 83.9 (Table 14). Overall, the vegetation of the mature dry sand prairie at Big River State Forest had a slightly lower similarity to

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Table 9. Frequency (%), mean cover (% of total cover), and importance value (I.V.) of the ground layer species encountered in 2004 in three plant communities at Ayers Nature Preserve, Carroll County, Illinois. (\*non-native species)

Species	Dry Sand Prairie (late successional) Area 10 (n=50)			Dry Sand prairie (mid-successional) Area 11 (n=50)			Blowing Sand (early successional) Area 12 (n=50)		
	Freq. %	Mean Cover	I. V.	Freq. %	Mean Cover	I. V.	Freq. %	Mean Cover.	I. V.
<i>Schizachyrium scoparium</i>	100	31.40	52.5	2	0.01	0.2	--	--	--
<i>Ambrosia psilostachya</i>	98	12.54	26.4	86	2.45	12.5	52	4.48	17.9
<i>Solidago nemoralis</i>	76	5.18	14.1	8	0.14	1.0	2	0.30	1.0
<i>Koeleria macrantha</i>	84	3.79	13.0	100	10.68	30.1	56	2.42	12.8
<i>Dichanthelium villosissimum</i>	72	2.08	9.6	100	14.16	37.0	84	6.60	27.3
<i>Carex muhlenbergii</i>	82	1.16	9.2	12	0.21	1.5	52	0.51	7.4
<i>Asclepias verticillata</i>	72	1.35	8.6	--	--	--	2	0.06	0.4
<i>Carex tonsa</i>	56	2.29	8.3	60	1.73	8.8	48	3.30	14.3
<i>Cyperus lupulinus</i>	68	0.94	7.6	4	0.02	0.4	8	0.04	1.0
<i>Polygala polygama</i>	64	0.62	6.8	34	0.52	4.0	2	0.01	0.2
<i>Aster ericoides</i>	26	2.60	6.0	--	--	--	--	--	--
<i>Callirhoe triangulata</i>	22	2.02	4.8	4	0.36	1.1	18	2.67	9.2
<i>Viola pedata</i>	22	0.99	3.4	--	--	--	36	0.92	6.5
<i>Conyza canadensis</i>	32	0.21	3.3	2	0.01	0.2	8	0.09	1.1
<i>Lespedeza capitata</i>	20	0.88	3.0	4	0.07	0.5	4	0.36	1.4
<i>Chrysopsis camporum</i>	16	0.81	2.6	6	0.13	0.8	--	--	--
<i>Panicum virgatum</i>	20	0.50	2.5	--	--	--	4	0.02	0.6
<i>Oenothera clelandii</i>	18	0.14	1.9	56	1.12	7.2	28	0.14	3.6
<i>Lithospermum croceum</i>	10	0.49	1.6	2	0.01	0.2	2	0.01	0.2
<i>Cyperus schweinitzii</i>	10	0.20	1.2	32	0.56	3.9	60	0.65	8.6
<i>Hieracium longipilum</i>	10	0.20	1.2	--	--	--	--	--	--
<i>Pseudognaphalium obtusifolium</i>	8	0.33	1.2	--	--	--	2	0.06	0.4
* <i>Achillea millefolium</i>	10	0.15	1.1	--	--	--	--	--	--
<i>Chenopodium dessicatum</i>	10	0.05	1.0	--	--	--	4	0.02	0.6
<i>Draba reptans</i>	10	0.10	1.0	68	1.09	8.2	--	--	--
<i>Selaginella rupestris</i>	6	0.32	1.0	--	--	--	--	--	--
<i>Leptoloma cognatum</i>	8	0.14	0.9	8	0.38	1.5	4	0.07	0.7
<i>Liatris aspera</i>	8	0.14	0.9	--	--	--	44	3.33	13.9
<i>Plantago patagonica</i>	8	0.04	0.8	4	0.02	0.4	--	--	--
<i>Chamaecrista fasciculata</i>	6	0.03	0.6	--	--	--	--	--	--
<i>Eragrostis spectabilis</i>	2	0.30	0.6	--	--	--	2	0.06	0.4
<i>Euphorbia corollata</i>	2	0.30	0.6	26	1.83	6.0	20	0.59	3.9
<i>Physalis virginiana</i>	4	0.07	0.5	14	0.07	1.3	18	0.14	2.5
<i>Aristida tuberculosa</i>	4	0.02	0.4	100	2.20	13.2	100	7.77	32.1
<i>Chamaesyce geyseri</i>	4	0.02	0.4	12	0.16	1.4	30	0.25	4.1
<i>Dichanthelium oligosanthes</i>	4	0.02	0.4	--	--	--	--	--	--
* <i>Mollugo verticillata</i>	4	0.02	0.4	60	0.70	6.7	22	0.11	2.8
<i>Froelichia gracilis</i>	2	0.01	0.2	--	--	--	--	--	--
* <i>Poa pratensis</i>	2	0.01	0.2	--	--	--	--	--	--
<i>Polygonella articulata</i>	2	0.01	0.2	50	0.40	5.2	42	0.61	6.4
<i>Croton glandulosus</i>	--	--	--	100	3.38	15.5	48	0.44	6.7
<i>Cyperus grayoides</i>	--	--	--	86	1.58	10.8	46	0.58	6.8
<i>Hudsonia tomentosa</i>	--	--	--	42	3.48	10.6	2	0.30	1.0
<i>Paspalum bushii</i>	--	--	--	20	2.23	6.3	12	0.50	2.7
<i>Diodia teres</i>	--	--	--	8	0.19	1.1	--	--	--
<i>Monarda punctata</i>	--	--	--	8	0.19	1.1	--	--	--
<i>Froelichia floridana</i>	--	--	--	6	0.03	0.6	6	0.08	0.9
<i>Asclepias viridiflora</i>	--	--	--	2	0.06	0.3	--	--	--
<i>Cycloloma atriplicifolium</i>	--	--	--	2	0.01	0.2	--	--	--
<i>Tradescantia ohiensis</i>	--	--	--	2	0.01	0.2	--	--	--
<i>Rhus aromatica</i>	--	--	--	--	--	--	2	0.06	0.4
<i>Apocynum sibericum</i>	--	--	--	--	--	--	2	0.01	0.2
Totals		72.47	200.0		50.19	200.0		37.56	200.0
Bare ground and litter		28.06			46.25			61.25	

Table 10. Frequency (%), mean cover (% of total cover), and importance value (I.V.) of the ground layer species encountered in 2004 in mature dry sand prairie and disturbed dry sand prairie communities at Thomson-Fulton Nature Preserve, Whiteside County, Illinois. (\*non-native species)

Species	Dry Sand Prairie (late successional)			Dry Sand prairie (early successional)		
	Area 13 (n=50)			Area 14 (n=50)		
	Frequency (%)	Mean Cover	I.V.	Frequency (%)	Mean Cover	I.V.
<i>Schizachyrium scoparium</i>	100	20.92	39.4	--	--	--
<i>Opuntia macrorhiza</i>	98	15.06	31.7	82	22.71	31.6
<i>Ambrosia psilostachya</i>	96	11.08	26.4	100	14.49	24.8
<i>Tephrosia virginiana</i>	50	12.22	21.9	26	3.77	6.4
<i>Dichanthelium villosissimum</i>	84	8.65	21.8	66	6.00	12.7
<i>Conyza canadensis</i>	88	1.13	12.8	82	3.53	11.6
<i>Callirhoe triangulata</i>	28	3.64	8.2	--	--	--
<i>Solidago nemoralis</i>	22	1.95	5.3	10	0.73	1.8
<i>Cyperus schweinitzii</i>	36	0.33	5.1	18	0.14	1.8
<i>Koeleria macrantha</i>	24	0.56	3.8	94	11.55	21.2
<i>Carex tonsa</i>	22	0.75	3.7	34	0.91	4.3
<i>Leptoloma cognatum</i>	12	1.08	3.0	12	1.08	2.3
<i>Cyperus lupulinus</i>	22	0.11	2.9	34	0.22	3.5
<i>Heterostipa spartea</i>	20	0.20	2.9	--	--	--
<i>Polygala polygama</i>	18	0.09	2.4	48	0.73	5.3
<i>Eragrostis spectabilis</i>	8	0.72	1.9	36	0.33	3.8
<i>Lespedeza capitata</i>	8	0.14	1.2	40	3.40	7.5
<i>Rhus aromatica</i>	2	0.30	0.7	2	0.30	0.5
* <i>Rumex acetosella</i>	6	0.03	0.7	10	0.39	1.4
<i>Polygonella articulata</i>	6	0.03	0.7	24	0.17	2.5
<i>Dichanthelium depauperatum</i>	4	0.12	0.7	--	--	--
<i>Aristida tuberculosa</i>	4	0.07	0.6	100	13.38	23.6
<i>Lithospermum croceum</i>	2	0.06	0.4	4	0.31	0.7
<i>Crotonopsis linearis</i>	2	0.01	0.3	14	0.07	1.5
<i>Panicum virgatum</i>	2	0.01	0.3	2	0.30	0.5
<i>Pseudognaphalium obtusifolium</i>	2	0.01	0.3	8	0.09	0.9
<i>Croton glandulosus</i>	2	0.01	0.3	56	0.33	5.8
<i>Lactuca canadensis</i>	2	0.01	0.3	10	0.10	1.1
<i>Physalis virginiana</i>	2	0.01	0.3	2	0.01	0.2
<i>Paspalum bishii</i>	--	--	--	84	9.06	17.6
<i>Carex mühlenbergii</i>	--	--	--	10	0.34	1.4
<i>Chrysopsis camporum</i>	--	--	--	6	0.66	1.3
<i>Oenothera clelandii</i>	--	--	--	12	0.06	1.3
<i>Liatris aspera</i>	--	--	--	2	0.30	0.5
<i>Monarda punctata</i>	--	--	--	4	0.02	0.4
<i>Froelichia floridana</i>	--	--	--	2	0.01	0.2
Totals	--	79.30	200.0	2	95.49	200.0
Bare ground and litter	--	22.12	--	--	6.88	--

the other study areas with a ISs of 36.9% with the blowout community at Lost Mound to a high of 59.5 with the *Schizachyrium/Poa* community at Lost Mound (Table 14). This area is nearly 120 km south of the other study areas (Fig. 1).

A PCA biplot explained 44.5% of the variance in the first two axes, and with 66% of the variance explained in four axes. The ordination biplot indicated sample data are widely scattered in ordination space; however, three groups can be discerned (Fig. 2). Discriminating the sample data into three groupings was supported by results from cluster analysis. One grouping includes transects from all sites included in the study (LM 3, LM 7, LM 8, Ay10, TF13, and BR15) and is positively correlated with *Schizachyrium scoparium*, the dominant

bunch grass in the sample transects and the species explaining the most variance on the first ordination axis. Associated species included *Ambrosia psilostachya*, *Eragrostis spectabilis*, *Lespedeza capitata*, *Monarda punctata*, *Opuntia macrorhiza*, *Polygala polygama*, and *Solidago nemoralis*. Another grouping comprised of transects from all sites except Big River (LM1, LM2, Ay11, Ay12, and TF14) is positively associated with species of blowouts and open sand habitats including *Hudsonia tomentosa*, *Panicum virgatum*, *Koeleria macrantha*, *Cyperus grayoides*, *Croton glandulosa*, *Polygonum articulata*, and *Aristida tuberculosa*. A third grouping is comprised solely of transects from Lost Mound (LM4, LM5, LM6, and LM9). Transects from this grouping are similar in that *S. scoparium* was missing or had

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Table 11. Frequency (%), mean cover (% of total cover), and importance value (I.V.) of ground layer species encountered in 2005 in a dry sand prairie community at Big River Natural Area, Henderson County, Illinois. (\*non-native species)

Species	Dry Sand Prairie (mature)		
	Area 15 (n=50)		
	Frequency (%)	Mean Cover	Importance Value
<i>Schizachyrium scoparium</i>	100	34.07	41.9
<i>Solidago nemoralis</i>	94	16.76	24.3
<i>Opuntia macrorhiza</i>	98	11.11	19.0
<i>Ambrosia psilostachya</i>	100	10.38	18.4
<i>Lespedeza capitata</i>	92	8.17	15.5
<i>Stylisma pickeringii</i>	46	7.24	10.9
<i>Monarda punctata</i>	94	2.38	10.0
<i>Dichanthelium villosissimum</i>	90	2.17	9.4
<i>Cyperus lupulinus</i>	94	0.47	8.1
<i>Commelina erecta</i>	76	0.83	6.9
<i>Carex muhlenbergii</i>	66	0.33	5.6
<i>Physalis virginiana</i>	40	1.33	4.5
<i>Leptoloma cognatum</i>	32	0.90	3.5
<i>Coryza canadensis</i>	30	0.15	2.6
<i>Cyperus schweinitzii</i>	28	0.14	2.4
<i>Paspalum bushii</i>	20	0.25	1.8
<i>Koeleria macrantha</i>	14	0.51	1.6
<i>Eragrostis spectabilis</i>	14	0.27	1.4
<i>Rhus glabra</i>	8	0.72	1.3
<i>Talinum rugospermum</i>	14	0.07	1.2
<i>Erigeron strigosus</i>	8	0.43	1.0
<i>Aristida tuberculosa</i>	10	0.05	0.8
<i>Plantago patagonica</i>	10	0.05	0.8
<i>Lithospermum croceum</i>	8	0.09	0.7
<i>Oenothera clelandii</i>	8	0.09	0.7
<i>Rhus aromatica</i>	4	0.36	0.7
<i>Chamaecrista fasciculata</i>	4	0.31	0.6
<i>Eragrostis trichodes</i>	6	0.13	0.6
<i>Euphorbia corollata</i>	4	0.31	0.6
<i>Cratogeomys linearis</i>	6	0.03	0.5
<i>Dichanthelium oligosanthes</i>	6	0.03	0.5
<i>Bouteloua hirsuta</i>	4	0.12	0.4
<i>Lactuca canadensis</i>	2	0.06	0.3
<i>Parthenocissus inserta</i>	2	0.06	0.3
<i>Pseudognaphalium obtusifolium</i>	2	0.06	0.3
<i>Quercus velutina</i>	2	0.06	0.3
* <i>Chenopodium album</i>	2	0.01	0.2
* <i>Poa pratensis</i>	2	0.01	0.2
<i>Solidago speciosa</i>	2	0.01	0.2
Totals		100.52	200.0
Bare ground and litter		10.72	



an IV less than 10%. However, these transects grouped differently depending on choices of distance measure and linkage method in cluster analysis, indicating they were only nominally similar. Many adventive species were present in this third grouping including *Achillea millefolium*, *Bromus inermis*, *Poa pratensis*, *Potentilla recta*, and *Rumex acetosella*. Also, a few native grass species that are not bunch forming are associated with these transects including *Sporobolus clandestinus*, *S. cryptandrus*, *Heterotheca spartea*, and *Triplasis purpurea*.

The ecological meaning in the ordination axes is unclear. Neither of the species scores on the first two axes are correlated with the perceived conservatism of species (coefficients of conservatism) or wetness coefficients. A multiple regression of site characteristics (parameters of sand prairie community: species density, species richness, adventive species richness, mean coefficient of conservatism, and percent bare ground) onto the first two ordination axes explained 30.5% of the variance in the species data and 66.8% of the variance in the fitted species data. Results from forward selection of these site characteristics indicated that only one, percent bare ground, explained a significant amount of the variation ( $P = 0.01$ , F-statistic 2.15). A triplot of species, sites, and site characteristics (not shown) indicated that percent bare ground was inversely associated with transects from Group 1 and positively associated with transects from Group 2.

## DISCUSSION

**Historical Summary:** Historical information on the sand deposits of northwestern Illinois comes from the work of Gleason in 1908 (Gleason 1910). This study was completed nine years before the establishment of the Savanna Army Depot in 1918. Most of the information in that study consisted of detailed species lists with only a small amount of qualitative descriptive information on a few of the more common associations. The annotated lists of the species encountered, as well as the species he found in each association, give some indication of the complexity of this extensive sand prairie. As Dr. Gleason was at Lost Mound for only three short visits during 1908 (31 May–3 June, 12–24 June, 15–18 August) he made no attempt to ensure that a complete collection or a complete list of this sand region was developed, and

many unusual locations for species were omitted (Gleason 1910).

Gleason (1910) described many of the plant associations and the successional processes that occur in the sand deposits throughout Illinois. His description of the Blowout Formation, its associations, and its succession to the Bunch-Grass Association are an excellent analysis of the complex and varied successional process in the sand deposits. He also described in detail the Mixed Consociates of the Bunch-Grass Association, which corresponds to the dry sand prairie community of White and Madany (1978). As described by Gleason (1910), this association was dominated by up to nine native bunch (clump) grasses and sedges, all common taxa of the sand deposits. Since the bunch grasses virtually excluded other growth beneath them, the remaining species of this association were restricted to the small areas of bare sand between the bunches. Gleason (1910) divided these secondary species into four ecological groups based on their habits and structure: large perennials and shrubs (that could compete with the bunch grasses); mat-plants (*Selaginella rupestris*, *Opuntia macrorhiza*); interstitials (mostly annuals with slender, frequently unbranched stems that were restricted to sand between the bunch grasses); and parasites (*Orobancha fasciculata*).

Since the early work of Gleason (1910), a few additional studies have been completed on the floristic composition and structure of the sand deposits of northwestern Illinois. In 1976 the Illinois Natural Areas Inventory (INAI) examined some of the sand prairies of this region (White 1978). During these studies frequency data were collected from 20 to 30 circular 0.25-m<sup>2</sup> plots located along transects. None of these data were published but the results are available from Illinois Department of Natural Resources, Springfield, Illinois. Bowles et al. (2003) used many of these INAI sites in their study concerning the use of fire in the management of sand prairie vegetation.

**Bunch-Grass Association of Gleason:** Gleason (1910) reported that the Mixed Consociates of the Bunch-Grass Association dominated the sand deposits of Illinois, including the Hanover area of northwestern Illinois and the Oquawka area in Henderson County. Common bunch grasses were *Koeleria macrantha*, *Leptoloma cognatum*, and *Schizachyrium scoparium*

Table 12. Size class density (#/ha), basal area (m<sup>2</sup>/ha), relative values, importance value (I.V.), and average diameter (cm) of the woody species encountered in 2005 in a degraded dry sand savanna community remnant at Big River Natural Area, Henderson County, Illinois. (\* non-native species)

Species	Seed-lings	Small Sap-lings	Large Sap-lings	Trees (#/ha)	Basal Area (m <sup>2</sup> /ha)	Rel. Den.	Rel. Dom.	I. V.	Av. Diam. (cm)
<i>Quercus velutina</i>	7500	1594	106	298	9.386	50.8	54.2	105.0	18.7
<i>Quercus marilandica</i>	1563	375	131	286	7.880	48.6	45.6	94.2	17.3
<i>Juniperus virginiana</i>	--	31	6	2	0.34	0.3	0.1	0.4	14.6
<i>Prunus serotina</i>	938	406	75	2	0.24	0.3	0.1	0.4	12.3
<i>Rubus allegheniensis</i>	3281	750	--	--	--	--	--	--	--
<i>Rubus occidentalis</i>	2031	1531	--	--	--	--	--	--	--
<i>Cornus drummondii</i>	1563	4250	--	--	--	--	--	--	--
<i>Celtis occidentalis</i>	1250	344	--	--	--	--	--	--	--
<i>Ribes missouriense</i>	781	438	--	--	--	--	--	--	--
<i>Rhus aromatica</i>	313	656	--	--	--	--	--	--	--
<i>Rhus glabra</i>	156	688	--	--	--	--	--	--	--
* <i>Elaeagnus umbellata</i>	--	31	--	--	--	--	--	--	--
<i>Gleditsia triacanthos</i>	--	31	--	--	--	--	--	--	--
* <i>Morus alba</i>	--	31	--	--	--	--	--	--	--
* <i>Rosa multiflora</i>	--	31	--	--	--	--	--	--	--
Totals	19376	11187	318	588	17.324	100.0	100.0	200.0	--

though all of the other graminoid taxa were also encountered, but rarely dominant. Overall, Gleason (1910) found that these three bunch grasses were “so regularly present and so frequently associated with each other that they may be regarded as the most typical grasses of the consocies.” Except on rare occasions where one or two of the bunch-grass species dominated a small area, the remaining grasses never occupied large portions of the ground space. Essentially all of the other species reported by Gleason (1910) for northwestern Illinois were found during the present study.

Patterns of bunch grasses diversity and abundance involve many factors and are scale and habitat dependent. All of the common bunch grasses of northern Illinois occur throughout these sand deposits, their presence in any particular area related to disturbance, moisture, and many other biotic and abiotic factors. Within the sand deposits of northwestern Illinois, the high-quality areas surveyed were mostly associated with the bunch grass *Schizachyrium scoparium*. This species was generally the dominant or subdominant species of these high-quality sites (Fig. 2). Also, these high-quality areas were negatively associated with exotic, non-native species. In contrast, areas of disturbance where blowing sand was common were positively associated with non-native species. The bunch grasses *Dichanthelium villosissimum*, *Koeleria macrantha*, and *Panicum virgatum* were positively associated with these areas of blowing sand (Fig. 2). In mid-successional areas, where many native sand prairie species were common, the concen-

tration of non-native species was highly variable, and many of the grasses present were not well-developed bunch grasses. Here *Dichanthelium oligosanthes*, *D. perlongum*, *Heterostipa spartea*, *Sporobolus clandestinus*, *S. crypan-drus*, *Triplasis purpurea*, and the non-native *Poa pratensis* were common. The mid-summer bunch grass *Leptoloma congatum* was positively associated with these mid-successional sites (Fig. 2).

Typical of the bunch-grass association, areas of bare ground and litter usually exist between the clumps. Generally the clumps of *Schizachyrium scoparium* were 15–40 cm across, nearly circular in outline, and formed dense masses. Some of the larger clumps of this species had dead centers forming rings in which no other species were observed. Most of the other common grasses of this bunch-grass association, particularly *Dichanthelium villosissimum* and *Koeleria macrantha*, had similar growth forms, but formed much smaller clumps. During the present study the mean cover of bare ground and litter in mature dry sand prairies was between 10% and 38%, in successional dry sand prairies between 6% and 30%, and in blowouts and blowing sand communities between 41% and 63%. Mature dry sand prairie communities in the Illinois River sand deposits of central Illinois also had extensive areas of open sand. At Long Branch Nature Preserve bare ground ranged from 38% to 44% in a mature dry sand prairie, while in a disturbed sand community bare ground averaged 59% (Phillippe et al. 2004). In another Mason County sand prairie complex at Henry



Allan Gleason Nature Preserve, bare ground and litter averaged 35% in a mature dry sand prairie, 47% to 52% in two successional communities, and 83% in a blowout community (McClain et al. 2004).

Between the clumps of grasses other graminoid species were common along with many prairie forbs. Though these sand prairies are part of the tallgrass prairie region, the species composition and relative abundance of the species in the interstitial areas between bunch grasses usually differ from those found in tallgrass prairies. Soil moisture retention of the sandy soil is low, and sand prairies generally support species that tolerate drier conditions. Also, productivity is generally low in sand prairies, due mostly to low soil organic matter content and low available nitrogen (Anderson et al. 1994). Very few native legumes were found in the communities studied. At Lost Mound, *Tephrosia virginiana* was the only native legume commonly encountered in the plots, other native legumes being rare. In contrast, at Ayers, Thomson/Fulton and Big River, both *Tephrosia virginiana* and *Lespedeza capitata* (round-headed bush clover) were relatively common, generally being among the top 10 species in IV.

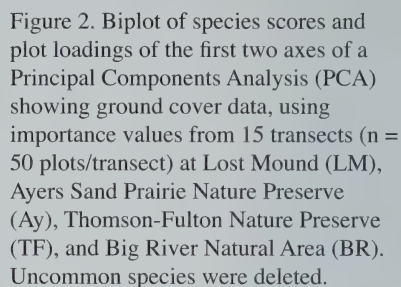
**Other Illinois Sand Deposits:** Sand prairie remnants have also been studied in the Green River Lowland Section of the Grand Prairie Natural Division in northwestern Illinois. These remnants are between 50 and 75 km east of the Mississippi River, are adjacent to the Mississippi River sand deposits, and were deposited during warm periods near the end of Wisconsinian Glaciation. One sand prairie remnant is on a shallow ridge surrounded by wet sand prairies and sedge meadows at the Richardson Wildlife Foundation (Handel et al. 2003). Here *Sorghastrum nutans* and *Schizachyrium scoparium* were dominant species, while the important forbs included *Euthamia graminifolia*, *Solidago nemoralis*, and *Liatris aspera*. The second sand prairie is associated with a dune ridge at Foley Sand Prairie Nature Preserve (McClain et al. 2003). Though *Schizachyrium scoparium* dominated this site, the remainder of the flora indicated more mesic conditions. On Foley sand prairie *Opuntia macrorhiza* was not encountered, *Dichanthelium villosissimum* was rare, and *Ambrosia psilostachya* was eighth in IV. Both prairie remnants were wetter than the sand prairies encountered in the Mississippi River sand deposits.

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Table 13. Summary of the variables for vegetation sample areas in the Mississippi River sand deposits of northwestern Illinois. (LM = Lost Mound; Ay = Ayers Sand Prairie Nature Preserve; TF = Thomson-Fulton Nature Preserve; BR = Big River State Forest)

Floristic summary data	Dry Sand prairie with <i>Schizachyrium scoparium</i> usually a dominant species								Dry Sand Prairie with <i>Schizachyrium scoparium</i> absent or poorly represented								Blowout, Blowing Sand, and Disturbance Communities, some cultivated in the past							
	LM3	LM7	LM8	Ay10	TF13	BR15	mean	LM4	LM5	LM6	LM9	mean	LM1	LM2	Ay11	Ay12	TF14	mean						
Native species richness	38	32	39	38	28	37	35.33	30	46	35	45	39.00	22	32	34	34	31	3.06						
Adventive species richness	4	8	6	10	1	12	8.83	2	7	3	5	4.25	7	8	11	8	1	1.20						
Species density per plot	9.66	8.90	11.58	10.62	7.72	12.42	10.15	7.18	14.42	11.16	12.16	11.23	7.24	8.06	11.30	7.72	10.34	9.13						
Total species richness	42	34	45	40	29	36	38.17	32	53	38	50	43.25	23	34	35	35	32	31.80						
Percent native	90.48	94.12	86.67	95.00	96.55	94.87	92.95	93.75	86.79	92.11	90.00	90.66	95.65	94.12	96.88	97.14	96.88	96.13						
Plant family number	18	15	21	19	12	19	17.33	14	22	17	23	19.00	11	14	21	19	14	15.80						
Cover bare ground & litter	30.36	22.99	26.70	28.06	22.12	10.72	23.49	16.82	13.08	22.36	38.10	22.59	63.04	40.60	46.25	61.25	6.88	43.60						
Floristic integrity index (FOI) (native species)	27.47	27.10	28.03	26.72	26.55	26.26	27.02	28.11	20.74	23.85	35.07	26.94	24.19	31.04	29.07	28.23	26.87	27.88						
Mean C-value	28.85	27.93	30.10	27.42	27.02	26.96	28.05	29.93	22.25	24.85	36.97	28.28	30.73	33.98	29.50	28.64	27.30	28.63						
Native mean C-value	4.24	4.65	4.18	4.23	4.93	4.21	4.41	4.97	3.85	3.87	4.96	4.57	5.04	5.32	4.91	4.77	4.75	4.96						
	4.68	4.94	4.82	4.45	5.11	4.43	4.74	5.30	3.28	4.20	5.51	4.57	5.27	5.66	5.06	4.91	4.90	5.16						





hudstom = *Hudsonia tomentosa*  
 ionalin = *Ionactis linariifolius*  
 koelmac = *Koeleria macrantha*  
 lactcan = *Lactuca canadensis*  
 leptcog = *Leptoloma cognatum*  
 lespcap = *Lespedeza capitata*  
 liatasp = *Liatris aspera*  
 litocro = *Lithospermum croceum*  
 mollver = *Mollugo verticillata*  
 monapun = *Monarda punctata*  
 oenocel = *Oenothera clelandii*  
 opunfra = *Opuntia fragilis*  
 opunmac = *Opuntia macrorhiza*  
 oxalstr = *Oxalis stricta*  
 panivir = *Panicum virgatum*  
 paspbus = *Paspalum bushii*  
 physvir = *Physalis virginiana*  
 planpat = *Plantago patagonica*  
 poaprat = *Poa pratensis*  
 polyart = *Polygonella articulata*  
 polypol = *Polygala polygama*  
 poterec = *Potentilla recta*  
 pseuobt = *Pseudognaphalium obtusifolium*  
 rhusaro = *Rhus aromatica*  
 rumeace = *Rumex acetosella*  
 schisco = *Schizachyrium scoparium*  
 selarup = *Selaginella rupestris*  
 solacar = *Solanum carolinense*  
 solinem = *Solidago nemoralis*  
 sorgnut = *Sorghastrum nutans*  
 sporcla = *Sporobolus clandestinus*  
 sporcry = *Sporobolus cryptandrus*  
 stylpic = *Stylisma pickeringii*  
 tephvir = *Tephrosia virginiana*  
 trippur = *Triplasis purpurea*  
 verbstr = *Verbena stricta*  
 violped = *Viola pedata*

Table 14. Similarity index of the dry sand prairies studied in the Mississippi River sand deposits of northwestern Illinois.

AREAS	Area 1	Area 2	Area 3	Area 4	Area 5	Area 6	Area 7	Area 8	Area 9	Area 10	Area 11	Area 12	Area 13	Area 14
Lost Mound – Area 1	1													
blowout comm.														
Lost Mound – Area 2	52.6													
blowing sand comm.														
Lost Mound – Area 3	43.1	65.8												
<i>Schizachyrium/Poa</i> comm.														
Lost Mound – Area 4	50.9	63.6	54.1											
<i>Tephrosia/Poa</i> comm.														
Lost Mound – Area 5	36.8	43.7	58.9	44.7										
Pinnus Prairie														
Lost Mound – Area 6	36.0	55.5	62.5	54.3	59.3									
<i>Sporobolus/Scelaginella</i> comm.														
Lost Mound – Area 7	45.6	64.7	65.8	63.6	43.7	52.8								
<i>Heterostipa/Oenothera</i> comm.														
Lost Mound – Area 8	44.1	58.2	64.4	54.5	55.1	65.1	53.2							
unburned dry sand prairie														
Lost Mound – Area 9	35.6	52.4	63.0	51.2	54.4	56.8	50.0	67.4						
burned dry sand prairie														
Ayers – Area 10	47.8	61.5	65.1	44.7	49.5	53.7	56.4	60.7	48.9					
mature dry sand prairie														
Ayers – Area 11	58.6	60.9	49.9	41.8	38.6	41.1	46.4	50.0	42.4	68.4				
disturbed dry sand prairie														
Ayers – Area 12	55.2	63.8	54.5	41.8	43.2	46.6	46.3	50.0	42.4	75.9	74.3			
blowing sand comm.														
Thomson-Fulton – Area 13	60.3	56.8	56.1	50.0	47.3	43.6	51.4	51.8	48.9	59.5	61.3	69.3		
mature dry sand prairie														
Thomson-Fulton – Area 14	66.7	59.2	55.7	43.5	48.9	45.3	45.1	53.7	46.0	59.3	66.7	83.9	80.5	
disturbed dry sand prairie														
Big River – Area 15														
mature dry sand prairie	36.9	52.6	59.5	43.2	44.2	57.5	47.4	52.9	45.7	48.8	51.9	51.9	53.7	55.7

The flora of the relatively mature dry sand prairie studied in the Mississippi River sand deposits is very similar to that of sand prairies associated with the Illinois River sand deposits in central Illinois. Dry sand prairies at Henry Allan Gleason Nature Preserve (McClain et al. 2004) and Long Branch Nature Preserve (Phillippe et al. 2004), both in Mason County, have nearly identical dominant species as those in northwestern Illinois. Both of these Mason County prairies were dominated by *Schizachyrium scoparium* while *Opuntia humifusa*, *Dichanthelium villosissimum*, and *Ambrosia psilostachya* were among the top six species in IV. Many subordinate species of these three dry sand prairies are also identical. In the mature dry sand prairies examined during the present study, many of the same species were high in IV. In many of the successional and disturbed communities examined during the present study, *Schizachyrium scoparium* was rarely encountered, though it was abundant throughout surrounding areas. The low incidence of this species may be related to its association with vesicular arbuscular mycorrhizal fungi that, for some reason, may not be present in the soil or may be due to the lack of certain soil nutrients (Dhillon et al. 1992, Anderson and Liberta 1992).

**Management Implications:** To study long-term changes in burned and unburned sand prairie remnants, many of the sites listed in the INAI were surveyed by Bowles et al. (2003) in 1996 and the results compared with the data obtained in the original INAI surveys. They studied seven sites: three that were managed with fire over the 20-year period and four that were not. Overall, native species richness per plot increased only on burned sites, whereas alien species richness per plot increased only on unburned sites. In the unburned sand prairies there was an increase in the alien grasses *Bromus inermis* and *Poa pratensis* that was accompanied by a decline in the native *Schizachyrium scoparium*, *Heterostipa spartea*, *Echinacea pallida*, *Helianthus pauciflorus*, and *Coreopsis palmata* (Bowles et al. 2003).

Similar results were observed during the present study, particularly at Lost Mound. Here fire suppression has been the rule since the army obtained the area in 1918 and adventive, cool-season grasses were planted into areas

of the prairie. Fire suppression has undoubtedly resulted in adventive species becoming important components of this dry sand prairie, particularly in high disturbance areas and successional communities. Presently fire is occasionally used in many of the nature preserves in the Mississippi River sand deposits, and at Lost Mound a burning program is being initiated since the land was transferred to the U.S. Fish and Wildlife Service in 2003 (Nýboer, personal observations). It is generally accepted that the establishment of prairie species is stimulated by fire and the removal of litter. Fires, as well as patch disturbances, generally increase species richness, particularly native prairie forbs that mostly occur as interstitial species in bunch-grass communities (Bowles et al. 2003). All available information indicates that fire, particularly early spring fires, are important in decreasing the extent of the cool-season, Eurasian grasses, decreasing the density and cover of adventive species, and increasing the density and cover of native sand prairie species.

**Adventive Species:** Presently adventive species are more abundant at Lost Mound than at the other natural areas examined. Adventive species are commonly associated with disturbances, particularly ground disturbances associated with human activity, such as roads, buildings, and agriculture, as well as overgrazing. At Lost Mound more than 100 adventive species were found associated with the prairie, mostly in areas of major disturbances. Within the plant communities studied at Lost Mound, adventive taxa were sometimes abundant. *Poa pratensis* was the most common adventive species in the study areas, being very abundant in the study plots in areas that had been heavily grazed in the past. Another commonly observed adventive grass was *Bromus inermis*, while *Rumex acetosella* and *Potentilla recta* were sometimes common in the study plots. At Ayers, Thomson/Fulton, and Big River, adventive species were less common. At these three sites *Poa pratensis* had an IV of 4.1 or lower within the plots. The only other adventive species encountered were *Achillea millefolium*, *Bromus tectorum*, *Chenopodium album*, *Mollugo verticillata*, and *Rumex acetosella*. Overall, in all of the natural areas examined, adventive species accounted for about 20% of the flora (Appendix I).



Few adventive legumes were recorded for the study plots. At Lost Mound, however, many were found in heavily disturbed areas, particularly along roadsides and in areas where cattle concentrations had been high (Appendix I). The most common adventive legume observed at Lost Mound was *Securigera varia* (crown vetch). Symstad (2004) found that the presence of crown vetch significantly increased soil nitrogen availability and significantly decreased native species richness and cover. High nitrogen levels caused a dramatic increase in *Poa pratensis* cover, which could hinder restoration efforts by competition with native species.

**Forest and Savanna Communities:** Gleason (1910) described the Lost Mound area as:

“The sand deposits are chiefly prairie, but a belt of forest lies along the river, and tongues and irregular areas of forest project out into the prairie, in some places extending nearly across.” Presently timber harvesting, grazing, oak wilt disease, and fire suppression have heavily modified the forest and savanna communities. A narrow belt of timber still exists along the river adjacent to Lost Mound. *Quercus velutina* dominates the dunes just back from the river, while a floodplain forest, dominated by *Acer saccharinum*, occurs on the frontal flats and the deposition area behind the navigation dam that crosses the Mississippi River near the north end of Lost Mound. On the sandy terrace behind the riverside dunes, prairie dominates. In this prairie scattered degraded savanna communities occur that are dominated by *Q. velutina*. In these sand forests and savannas, overstory species diversity is relatively low with *Q. velutina* the dominant species on dry sites and *Q. alba* becoming an important component of moister sites. At Big River State Forest, *Q. marilandica* becomes an important overstory component in the dry sand forest.

Throughout the sand deposits of Illinois, *Quercus velutina* generally dominates with none or only a few other *Quercus* species and sometimes with a few species of the genus *Carya* (hickories). In the Kankakee River sand deposits dry to dry-mesic sand savanna and forests communities are dominated by *Q. velutina*, which accounted for 75% to 97% of

the IV. On more mesic sites *Q. alba* was the only other tree species commonly encountered (Johnson and Ebinger 1992). In the Illinois River sand deposits, in contrast, overstory species diversity is sometimes higher. Again *Q. velutina* is the dominant species, but *Q. marilandica* is usually well established along with occasional individuals of *Carya texana* (black hickory) and *C. tomentosa* (mockernut hickory) (McClain et al. 2002). The forest communities in the Big River State Forest, though heavily degraded by fire suppression, are similar to the dry sand forests of the Illinois River sand deposits.

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## APPENDIX I

Vascular plant species found in the Lost Mound Unit Savanna District of the Upper Mississippi River National Wildlife and Fish Refuge, Ayers Sand Prairie Nature Preserve, Thomson-Fulton Nature Preserve, and Big River State Forest, are listed alphabetically by family under major plant groups. An asterisk indicates non-native species. Collecting numbers preceded by G were collected by Henry A. Gleason and are deposited in the University of Illinois Herbarium, Urbana, Illinois (ILL). Collecting numbers preceded by P or S were collected by Loy R. Phillippe or Amy Symstad and are deposited in the Illinois Natural History Survey Herbarium, Champaign, Illinois (ILLS). Collecting numbers preceded by E were collected by John E. Ebinger and are deposited in the Eastern Illinois University Herbarium, Charleston, Illinois (EIU). In addition, a few of the species were observed but not collected, and a few were reported by the Illinois Natural Areas Inventory (INAI) for which we could not find vouchers. The letter after each collecting number indicates the collecting site: s = Lost Mound; a = Ayers Sand Prairie Nature Preserve; t = Thomson-Fulton Nature Preserve; b = Big River State Forest.

### FERNS AND FERN-ALLIES

#### Aspleniaceae

*Asplenium platyneuron* (L.) Oakes: P27959s

#### Dennstaedtiaceae

*Pteridium aquilinum* (L.) Kuhn: P28006s

#### Dryopteridaceae

*Athyrium filix-femina* (L.) Martens ssp. *angustum* (Willd.) R.T. Clausen: P27491s

*Cystopteris protrusa* (Weatherby) Blasdell: P27794s

*Dryopteris carthusiana* (Villars) H.P. Fuchs: P27487s

*Woodsia obtusa* (Spreng.) Torr.: P28578s

#### Equisetaceae

*Equisetum arvense* L.: P27198s

*Equisetum x ferrissii* Clute: P28587s

*Equisetum hyemale* L.: P27812s

*Equisetum laevigatum* A. Br.: P27529s; P36240a; E30652t

*Equisetum pratense* Ehrh.: P27195s

#### Onocleaceae

*Onoclea sensibilis* L.: P28270s

#### Ophioglossaceae

*Botrychium dissectum* Spreng.: P28441s

*Botrychium virginianum* (L.) Sw.: P27483s

*Ophioglossum pusillum* Raf.: P28440s

#### Osmundaceae

*Osmunda claytoniana* L.: P28449s

#### Pteridaceae

*Adiantum pedatum* L.: P27485s

#### Selaginellaceae

*Selaginella rupestris* (L.) Spring.: P27158s; E30611a; E31566t

## GYMNOSPERMS

### Cupressaceae

*Juniperus virginiana* L.: P27503s; E31263a; E30599t; E31667b

### Pinaceae

\**Pinus banksiana* Lamb.: P28581s; E30600t; E31952b

\**Pinus resinosa* Ait.: P28446s

\**Pinus sylvestris* L.: P37108a; E31231t

## MONOCOTS

### Agavaceae

\**Yucca smalliana* Fern.: E31567t

### Alismataceae

*Alisma subcordatum* Raf.: P27974s

*Sagittaria latifolia* Willd.: M3411; P28238s

### Araceae

*Arisaema dracontium* (L.) Schott: P27488s

*Arisaema triphyllum* (L.) Schott: P27201s

### Commelinaceae

*Commelina erecta* L.: P27849s; INA1a; E31378t; E31467b

*Tradescantia ohiensis* Raf.: P27424s; E30628a; E30653t; E31699b

### Cyperaceae

*Bolboschoenus fluviatilis* (Torr.) Sojak: P28569s

*Bulbostylis capillaris* (L.) C.B. Clarke: P27832s; P37248b

*Carex bicknellii* Britt.: P27408s; E30630a

*Carex blanda* Dewey: P27280s

*Carex brachyglossa* Mack.: P27518s

*Carex brevior* (Dewey) Mack.: P27420s

*Carex cephalophora* Muhl. ex Willd.: E31867b

*Carex conjuncta* Boott: P27434s

*Carex cristatella* Britt.: P27810s

*Carex duriuscula* C.A. Meyer: P27326s

*Carex festucacea* Schk.: E31376a; P36717t

*Carex frankii* Kunth: P27963s

*Carex gravida* L.H. Bailey: P27498s

*Carex grayi* Carey: P27453s

*Carex grisea* Wahl: P27452s

*Carex hirtifolia* Mack.: P27472s

*Carex hystericina* Muhl.: P27494s

*Carex laeviconica* Dewey: P27796s

*Carex lupulina* Willd.: P27552s

*Carex meadii* Dewey: P27209s

*Carex molesta* Mack.: P27517s

*Carex muhlenbergii* Schk.: P27425s; E30629a; E30654t; E31468b

*Carex pensylvanica* Lam.: P27211s; E31321a; E31311t; E31664b

*Carex rosea* Schk.: P27437s

*Carex scoparia* Schk.: P27438s



*Carex stipata* Muhl.: P27471s  
*Carex stricta* Lam.: P27430s  
*Carex tonsa* (Fern.) Bickn.: P27159s; E31320a; E31379t  
*Carex tribuloides* Vahl: P27551s  
*Carex typhina* Michx.: P27792s  
*Carex vulpinoidea* Michx.: P27756s  
*Cyperus erythrorhizos* Muhl.: P28085s  
*Cyperus esculentus* L.: P28084s  
*Cyperus grayoides* Mohlenbr.: P27829s; P37104a; E31509t  
*Cyperus lupulinus* (Spreng.) Marcks var. *lupulinus*: P27512s; P36211a; E31508t; E31865b  
*Cyperus lupulinus* (Spreng.) Marcks var. *macilentus* (Fern.) Marcks: P27718s; E31864b  
*Cyperus x mesochorus* Geise: E31866b  
*Cyperus odoratus* L.: P28044s  
*Cyperus schweinitzii* Torr.: P27717s; E31709a; E31380t; E31469b  
*Cyperus squarrosus* L.: P28226s  
*Eleocharis acicularis* (L.) Roem. & Schultes: P27543s  
*Eleocharis erythropoda* Steud.: P28120s  
*Eleocharis ovata* (Roth) Roem. & Schultes var. *obtusata* (Willd.) Kukenth: P27975s  
*Scirpus atrovirens* Willd.: P27783s  
*Scirpus cyperinus* (L.) Kunth: P27981s

### Hydrocharitaceae

*Elodea nuttallii* (Planch.) St. John: P28242s  
*Vallisneria americana* Michx.: P28245s

### Iridaceae

*Iris shrevei* Small: P27800s  
*Sisyrinchium albidum* Raf.: E31322a; E31470b  
*Sisyrinchium campestre* Bickn.: P27300s; E31665b  
*Sisyrinchium mucronatum* Michx.: E31323a

### Juncaceae

*Juncus interior* Wieg.: P27782s  
*Juncus tenuis* Willd.: P27757s

### Lemnaceae

*Lemna minor* L.: P28095s  
*Spirodela polyrrhiza* (L.) Schleiden: P28264.1s  
*Wolffia columbiana* Karst: P28264.2s

### Liliaceae

*Allium canadense* L.: P27788s  
\**Asparagus officinalis* L.: P27457s  
\**Hemerocallis fulva* (L.) L.: P27815s  
*Polygonatum commutatum* (Schult.) A. Dietr.: P27716s  
*Polygonatum biflorum* (Walt.) Ell.: E31700b  
*Smilacina stellata* (L.) Desf.: P27166s

### Najadaceae

*Najas minor* All.: P27814s

**Orchidaceae**

*Galearis spectabilis* (L.) Raf.: P27332s

*Liparis liliifolia* (L.) Rich.: P28439s

*Spiranthes lacera* (Raf.) Raf.: S364s

**Poaceae**

*Agrostis gigantea* Roth: P27761s

*Agrostis hyemalis* (Walt.) BSP.: P27509s; INA1a

*Alopecurus carolinianus* Walt.: P27440s

*Andropogon gerardii* Vitman: P28108s; E31264a; INAIt; E31954b

*Aristida basiramea* Engelm.: P328114s; P36235a

*Aristida oligantha* Michx.: P28112s

*Aristida tuberculosa* Nutt.: P28028s; E31265a; E31232t; P37242b

*Bouteloua curtipendula* (Michx.) Torr.: P27864s

*Bouteloua gracilis* (HBK.) Lag.: P28554s

*Bouteloua hirsuta* Lag.: P27940s; P36216a; INAIt; E31855b

\**Bromus inermis* Leyss.: P27499s; E30631a; E30656t; E31701b

*Bromus kalmii* Gray: P28101s

\**Bromus racemosus* L.: P27502s; E30655t

\**Bromus tectorum* L.: P27311s; E30612a; E30601t; E31856b

*Calamovilfa longifolia* (Hook.) Scribn.: P28424s; E31266a; E31233t; E31471b

*Cenchrus longispinus* (Hack.) Fern.: P27968s; INA1a; INAIt; E31857b

\**Chloris verticillata* Nutt.: P27732s

*Cinna arundinacea* L.: P28433s

\**Dactylis glomerata* L.: P27470s

*Dichanthelium acuminatum* (Sw.) Gould & Clark var. *fasciculatum* (Torr.) Freckm.: P27713s

*Dichanthelium acuminatum* (Sw.) Gould & Clark var. *implicatum* (Scribn.) Gould & Clark: P28129s

*Dichanthelium depauperatum* (Muhl.) Gould: P27422s; P37099t

*Dichanthelium linearifolium* (Scribn.) Gould: P27527s

*Dichanthelium oligosanthos* (Schult.) Gould: P27423s; E30633a; E30659t; E31472b

*Dichanthelium perlongum* (Nash) Freckm.: E31936a

*Dichanthelium villosissimum* (Nash) Freckm.: P27414s; E30634a; E30658t; E31473b

*Dichanthelium wilcoxianum* (Vasey) Freckm.: S337s

*Digitaria filiformis* (L.) Koel.: P37243b

\**Digitaria ischaemum* (Screb.) Schreb.: E31510t

\**Digitaria sanguinalis* (L.) Scop.: P27917s; E31858b

\**Echinochloa crus-galli* (L.) P. Beauv.: P27980s

*Echinochloa muricata* (Michx.) Fern.: P28053s

\**Eleusine indica* (L.) Gaertn.: E31859b

*Elymus canadensis* L.: P27781s; E31511t

*Elymus trachycaulus* (Link) Gould: P27949s

*Elymus virginicus* L.: P27998s

\**Elytrigia repens* (L.) Desv.: P27947s; E31710a; INAIt

\**Elytrigia smithii* (Rydb.) Nevski: P27496s

\**Eragrostis cilianensis* (All.) Vign.: P28213s

*Eragrostis hypnoides* (Lam.) BSP: P28044s

\**Eragrostis minor* Host: P27778s

*Eragrostis pectinacea* (Michx.) Nees: P27836s

*Eragrostis spectabilis* (Pursh) Steud.: P27742s; P36231a; E31234t; E31955b

*Eragrostis trichodes* (Nutt.) Wood: P28284s; P37233b

\**Festuca arundinacea* Schreb.: P27492s

\**Festuca pratensis* Huds.: P27410s

*Festuca subverticillata* (Pers.) E.B. Alexeev: P27468s

\**Festuca trachyphylla* (Hack.) Krajina: P27554s

*Glyceria striata* (Lam.) Hitchc.: P27482s

*Heterostipa spartea* (Trin.) Barkworth: P27412s; E30636a; E30660t; E31702b

*Hordeum jubatum* L.: P27548s

*Koeleria macrantha* (Ledeb.) Spreng.: P27421s; E30632a; E30602t; E31474b

*Leersia oryzoides* (L.) Swartz: P28043s

*Leersia virginica* Willd.: P28081s

*Leptoloma cognatum* (Schult.) Chase: P27916s; P36197a; E31512t; E31475b

\**Lolium perenne* L.: P27513s

*Muhlenbergia mexicana* (L.) Trin.: P28435s

*Muhlenbergia racemosa* (Michx.) BSP: P28277s

*Muhlenbergia schreberi* J.F. Gmel.: P28434s

*Panicum capillare* L. var. *capillare*: P28054s; E31513t; E31860b

*Panicum virgatum* L.: P27986s; E31269a; E31235t

*Paspalum bushii* Nash: P27859s; P36215a; E31514t; E31476b

*Paspalum setaceum* Michx. var. *ciliatifolium* (Michx.) Vasey: P28066s; P36232a; INAlt; E31861b

\**Phalaris arundinacea* L.: P27439s

\**Poa bulbosa* L.: P27324s

\**Poa compressa* L.: P27419s; E31711a; INAlt

*Poa palustris* L.: P27493s

\**Poa pratensis* L.: P27307s; E30635a; E30661t; E31666b

*Schizachyrium scoparium* (Michx.) Nash: P28425s; E31267a; E31236t; P37237b

\**Setaria faberi* R.A.W. Herrm.: P28069s; E31515t; E31863b

\**Setaria glauca* (L.) P. Beauv.: P28051s; P36213a; E31862b

\**Setaria viridis* (L.) P. Beauv.: P27725s

*Sorghastrum nutans* (L.) Nash: P28035s; P36206a; E31516t; P37246b

*Spartina pectinata* Link: P27997s; E31270a

*Sphenopholis intermedia* (Rydb.) Rydb.: P27486s

*Sphenopholis obtusata* (Michx.) Scribn.: P27514s

*Sporobolus clandestinus* (Biehler) Hitchc.: P28223s

*Sporobolus compositus* (Poir.) Merr.: P28418s; E31271a

*Sporobolus cryptandrus* (Torr.) Gray: P27511s; P36194a; P36160t; E31953b

*Sporobolus heterolepis* (Gray) Gray: INAlt

*Sporobolus vaginiflorus* (Torr.) A. Wood: P28212s; E31237t

*Tridens flavus* (L.) Hitchc.: P28090s; P37249b

*Triplasis purpurea* (Walt.) Chapm.: P28062s; P36230a; P366187t; P37250b

\**Triticum aestivum* L.: P27764s

*Vulpia octoflora* (Walt.) Rydb.: P27303s; P36708a; E30662t

### **Pontederiaceae**

*Zosterella dubia* (Jacq.) Small: P28259.1s

### **Potamogetonaceae**

\**Potamogeton crispus* L.: P28243s

*Potamogeton nodosus* Poir.: P27544s

*Potamogeton pusillus* L.: P28259.2s

*Stuckenia pectinata* (L.) Borner: P28258s

### **Smilacaceae**

*Smilax lasioneuron* Hook.: P27813s

*Smilax tamnoides* L.: P27426s

### **Sparganiaceae**

*Sparganium eurycarpum* Engelm.: P27984s



**Typhaceae**

*Typha latifolia* L.: P28442s

**Zannichelliaceae**

*Zannichellia palustris* L.: P28590s

**DICOTS****Acanthaceae**

*Ruellia humilis* Nutt.: P27838s; E31822b

**Aceraceae**

*Acer negundo* L.: P27277s; P36709a; E31381t

*Acer saccharinum* L.: P27208s

*Acer saccharum* Marsh.: P28588s

**Amaranthaceae**

*Amaranthus rudis* J. Sauer: P28235s

\**Amaranthus spinosus* L.: P28430s

*Amaranthus tuberculatus* (Moq.) Sauer: P28432s

*Froelichia floridana* (Nutt.) Moq.: P27830s; P36210a; E31238t; E31823b

*Froelichia gracilis* (Hook.) Moq.: P27706s; E31937a; E31239t; E31446b

**Anacardiaceae**

*Rhus aromatica* Ait. var. *arenaria* (Greene) Fern.: P27320s; E31447b

*Rhus aromatica* Ait. var. *aromatica*: P27951s; E30613a; E30603t

*Rhus glabra* L.: P27334s; INAIa; P36190t; E31824b

*Rhus hirta* L.: P36223a; E31240t

*Toxicodendron radicans* (L.) Kuntze: P27719s; P36233a; E31241t; E31668b

**Apiaceae**

*Cicuta maculata* L.: P27993s

\**Conium maculatum* L.: P27768s

*Cryptotaenia canadensis* (L.) DC.: P27786s

\**Daucus carota* L.: P27726s; E31825b

*Eryngium yuccifolium* Michx.: INAI t

*Heracleum maximum* Bartr.: P27429s

*Osmorhiza claytonii* (Michx.) C.B. Clarke: P27436s

*Osmorhiza longistylis* (Torr.) DC.: P27435s

\**Pastinaca sativa* L.: P27791s

*Sanicula canadensis* L.: P27711s

*Sanicula odorata* (Raf.) Pryer & Phillippe: P27469s

*Spermolepis inermis* (Nutt.) Math. & Constance: P27739s; E31377a

**Apocynaceae**

*Apocynum sibiricum* Jacq.: P28086s; P36222a

**Araliaceae**

*Aralia nudicaulis* L.: P27845s

**Asclepiadaceae**

- Asclepias amplexicaulis* Small: P27522s; E31359a; E31382t; E31826b  
*Asclepias hirtella* (Pennell) Woodson: P36221a; P36166t  
*Asclepias incarnata* L.: P27988s  
*Asclepias syriaca* L. var. *syriaca*: P27704s; E31360a; E31383t; E31669b  
*Asclepias tuberosa* L.: P27945s  
*Asclepias verticillata* L.: P27946s; P36195a; E31384t; E31448b  
*Asclepias viridiflora* Raf.: P27703s; E31361a; E31385t; E31449b

**Asteraceae**

- \**Achillea millefolium* L.: P27507s; E30637a; E30663t; E31670b  
*Ageratina altissima* (L.) R.M. King & H. Rob.: P27966s  
*Ambrosia artemisiifolia* L.: P28070s; P36209a; E31477t; E31827b  
*Ambrosia psilostachya* DC.: Observed at s; E31275a; E31242t; E31828b  
*Ambrosia trifida* L.: P28092s  
*Antennaria neglecta* Greene: P27183s; E31312t  
*Antennaria plantaginifolia* (L.) Hook.: P28118s; P36713a; E31647b  
\**Arctium lappa* L.: P27954s  
\**Arctium minus* Schk.: P28131s  
*Artemisia campestris* L.: P28117s; E31478t  
\**Artemisia ludoviciana* Nutt.: P28286s  
*Aster cordifolius* L.: P28596s  
*Aster ericoides* L.: P28252s; E31274a; E31243t  
*Aster lanceolatus* Willd.: P28232s  
*Aster lateriflorus* (L.) Britt.: P28448s  
*Aster oblongifolius* Nutt.: P28283s  
*Aster ontarionis* Wieg.: P28234s  
*Aster oolentangiensis* Riddell: P28423s  
*Aster pilosus* Willd.: Observed at s; E31273a; E31245t; E31956b  
*Aster prenanthoides* Muhl.: P28271s  
*Aster puniceus* L.: P28444s  
*Aster sericeus* Vent.: P28214s; INA1a; E31244t  
*Bidens bipinnata* L.: E31829b  
*Bidens cernua* L.: P28229s  
*Bidens comosa* (Gray) Wieg.: P28228s  
*Bidens vulgata* Greene: P28123s  
*Brickellia eupatorioides* (L.) Shinnars: P28218s; P36224a; E31246t; P37234b  
\**Carduus nutans* L.: P27541s; E31671b  
\**Centaurea biebersteinii* DC.: P27846s  
*Chrysopsis camporum* Greene: P27533s; E30638a; E30665t  
\**Cirsium arvense* (L.) Scop.: P27777s  
*Cirsium discolor* (Muhl.) Spreng.: P28050s; P36196a; E31479t  
\**Cirsium vulgare* (Savi) Tenore: P27943s  
*Conyza canadensis* (L.) Cronq.: P28036s; E31276a; E31247t; P37231b  
*Coreopsis palmata* Nutt.: P27715s; P36207a; E31386t; E31451b  
\**Crepis tectorum* L.: P27557s  
*Echinacea pallida* (Nutt.) Nutt.: Observed at s; INAIt; E31453b  
*Eclipta prostrata* (L.) L.: P28248s  
*Erechtites hieracifolia* (L.) Raf.: P28225s  
*Erigeron annuus* (L.) Pers.: P27497s; E31961a  
*Erigeron philadelphicus* L.: P27432s  
*Erigeron strigosus* Muhl.: P27520s; E31362a; E30664t; E31452b  
*Eupatoriadelphus purpureus* (L.) R.M. King & H. Rob.: P27989s  
*Eupatorium perfoliatum* L.: P27990s

*Eupatorium serotinum* Michx.: P27970s  
*Euthamia graminifolia* (L.) Nutt.: E31480t  
 \**Grindelia squarrosa* (Pursh) Dunal: P28059s  
*Helenium autumnale* L.: P28072s  
 \**Helianthus annuus* L.: P27720s  
*Helianthus hirsutus* Raf.: P28603s  
*Helianthus mollis* Lam.: P28061s  
*Helianthus occidentalis* Riddell: P27924s; P36202a; E31481t; E31830b  
*Helianthus pauciflorus* Nutt.: P28111s; E31250t; P37238b  
 \**Helianthus petiolaris* Nutt.: P36220a; P36172t; E31831b  
*Helianthus strumosus* L.: E31454b  
*Helianthus tuberosus* L.: P28107s  
*Heliopsis helianthoides* (L.) Sweet: P27952s  
*Hieracium longipilum* Torr.: P27935s; P36203a; E31482t  
*Ionactis linariifolius* (L.) Greene: P28568s; E31272a; INAIIt  
*Krigia virginica* (L.) Willd.: P27177s; E31324a; E30604t; E31648b  
*Lactuca canadensis* L.: P28445s; P36198a; E31483t; P37236b  
*Lactuca floridana* (L.) Gaertn.: P28103s  
 \**Lactuca serriola* L.: P28064s; E31484t; E31832b  
*Liatris aspera* Michx.: P28032s; E31278a; E31251t  
 \**Matricaria discoidea* DC.: P27779s  
*Oligoneuron rigidum* (L.) Small: P28217s  
*Pseudognaphalium obtusifolium* (L.) Hilliard & Burt: P28034s; E31277a; E31248t; E31951b  
*Ratibida pinnata* (Vent.) Barnh.: P27987s  
*Rudbeckia hirta* L.: P27730s; E31704a; E31672b  
*Rudbeckia laciniata* L.: P28106s  
*Rudbeckia triloba* L.: P28105s  
*Senecio plattensis* Nutt.: P27164s; P36715a; E31649b  
*Silphium perfoliatum* L.: P28099s  
*Solidago canadensis* L.: P28077s; E31485t  
*Solidago juncea* Ait.: INAIIt  
*Solidago gigantea* Ait.: P28080s  
*Solidago nemoralis* Ait.: P27958s; E31279a; E31252t; P37235b  
*Solidago speciosa* Nutt.: P28267s; INAIa; INAIIt; E31455b  
*Solidago ulmifolia* Muhl.: P28566s  
 \**Taraxacum officinale* Weber: P27312s  
 \**Tragapogon dubius* Scop.: P27411s; E30639a; E30666t; E31673b  
*Vernonia fasciculata* Michx.: P28073s

### Balsaminaceae

*Impatiens capensis* Meerb.: P28037s  
*Impatiens pallida* Nutt.: P28005s

### Berberidaceae

\**Berberis thunbergii* DC.: P28001s  
*Podophyllum peltatum* L.: P27283s

### Betulaceae

*Betula nigra* L.: P27161s

### Bignoniaceae

\**Catalpa speciosa* Warder: P28121s; E31387t



**Boraginaceae**

\**Cynoglossum officinale* L.: P27463s

\**Echium vulgare* L.: P27500s

*Hackelia virginiana* (L.) I.M. Johnston: P27919s

\**Lappula squarrosa* (Retz.) Dumort.: P27769s

*Lithospermum croceum* Fern.: P27163s; E30614a; E30605t; E31652b

*Lithospermum incisum* Lehm.: P27299s; INA1a; E31313t

**Brassicaceae**

\**Alliaria petiolata* (Bieb.) Cavara & Grande: P27310s

\**Alyssum alyssoides* (L.) L.: P27289s

*Arabis canadensis* L.: P27465s

*Arabis divaricarpa* A. Nelson: P27556s

*Arabis glabra* (L.) Bernh.: P27343s; E30640a; E31314t

*Arabis lyrata* L.: P27154s; E30615a; E30606t; E31650b

\**Barbarea vulgaris* R. Br.: P27342s

\**Berteroa incana* (L.) DC.: P27449s

\**Brassica nigra* (L.) Koch: P27738s

\**Capsella bursa-pastoris* (L.) Medic.: P27279s

*Cardamine bulbosa* (Muhl.) BSP: P27331s

\**Cardamine hirsuta* L.: P27433s

*Cardamine parviflora* L.: P27309s

*Cardamine pennsylvanica* Willd.: P28239s

*Descurainia pinnata* (Walt.) Britt.: P27165s; E30616a; E30667t; E31651b

\**Draba nemorosa* L.: P27284s

*Draba reptans* (Lam.) Fern.: P27156s; E31325a; E30668t

\**Eriophila verna* (L.) Chev.: P27191s; E31565t

\**Erysimum cheiranthoides* L.: E30670t

\**Erysimum inconspicuum* (S. Wats.) MacM.: P27416s

\**Lepidium campestre* (L.) R. Br.: P27407s

\**Lepidium densiflorum* Schrad.: P27409s; E31363a; E30669t; E31833b

*Lepidium virginicum* L.: P27302s; E30617a

*Rorippa sessiliflora* (Nutt.) A. Hitchc.: P27450s

\**Rorippa sylvestris* (L.) Besser: P27535s

\**Sisymbrium altissimum* L.: P27293s

\**Thlaspi arvense* L.: P27204s

**Cactaceae**

*Opuntia fragilis* (Nutt.) Haw.: P28065s

*Opuntia macrorhiza* Engelm.: P27862s; E31253t; E31445b

**Caesalpinaceae**

*Chamaecrista fasciculata* (Michx.) Greene: P27934s; P36192a; E31487t; E31834b

*Gleditsia triacanthos* L.: P27417s; E31365a; E31488t; E31674b

*Gymnocladus dioica* (L.) K. Koch: P27805s

**Campanulaceae**

*Campanulastrum americanum* (L.) Small: P27809s

*Lobelia cardinalis* L.: P27999s

*Lobelia inflata* L.: P28126s

*Lobelia siphilitica* L.: P28091s

*Triodanis perfoliata* (L.) Nieuwl.: P27505s; E30641a; E30671t; E31675b

**Cannabinaceae**

\**Cannabis sativa* L.: P27833s; E31935a

\**Humulus japonicus* Sieb. & Zucc.: P28285s

*Humulus lupulus* L.: P28124s

**Capparaceae**

*Polanisia dodecandra* (L.) DC.: P27737s; E31456b

*Polanisia jamesii* (Torr. & Gray) Iltis: P27714s

**Caprifoliaceae**

\**Lonicera morrowii* Gray: P27295s; E31327a; P36182t

\**Lonicera tatarica* L.: P27281s; E31328a

\**Lonicera xylosteum* L.: E31676b

*Sambucus canadensis* L.: P27766s

*Viburnum lentago* L.: P27323s

\**Viburnum opulus* L.: P27428s

**Caryophyllaceae**

\**Arenaria serpyllifolia* L.: P27305s; E30644a; E31653b

\**Cerastium brachypodum* (Engelm.) B.L. Robins.: P27181s

\**Cerastium fontanum* Baum.: P27315s

\**Dianthus armeria* L.: P27775s

\**Holosteum umbellatum* L.: P27184s; E30618a; E31630b

\**Myosoton aquaticum* (L.) Moench.: P27442s

*Paronychia canadensis* (L.) Wood: P27831s

*Paronychia fastigiata* (Raf.) Fern.: P27921s

\**Saponaria officinalis* L.: P27707s; E31677b

*Silene antirrhina* L.: P27418s; E30643a; E30643t; E31679b

\**Silene cserei* Baumg.: P27418s; E30672t

\**Silene dioica* (L.) Clairv.: E31678b

*Silene nivea* (Nutt.) Otth.: P27787s

\**Silene pratensis* (Spreng.) Godron & Gren: P27526s; E30642a

\**Stellaria media* (L.) Cyrillo: S227s

**Celastraceae**

*Celastrus scandens* L.: P27427s; E30645a; E31836b

*Euonymus atropurpureus* Jacq.: P28597s

**Ceratophyllaceae**

*Ceratophyllum demersum* L.: P28240s

**Chenopodiaceae**

\**Chenopodium album* L.: P36204a; E31388t; E31457b

\**Chenopodium ambrosioides* L.: P28048s

*Chenopodium desiccatum* A. Nels.: E31280a

*Chenopodium pratericola* Rydb.: P28049s

*Chenopodium simplex* (Torr.) Raf.: P27834s

*Cycloloma atriplicifolium* (Spreng.) Coult.: P27736s; E31939a; E31680b

\**Salsola collina* Pallas: P28115s; E31486t

**Cistaceae**

- Helianthemum bicknellii* Fern.: P27851s; P36241a; P37241b  
*Helianthemum canadense* (L.) Michx.: P27456s; E30646a; P36716t  
*Hudsonia tomentosa* Nutt.: P27460s; E31326a  
*Lechea pulchella* Raf.: P27867.2s  
*Lechea tenuifolia* Michx.: P27868.1s; P37239b

**Convolvulaceae**

- Calystegia sepium* (L.) R. Br.: P27767s  
\**Convolvulus arvensis* L.: P27852s  
*Stylisma pickeringii* (Torr.) Gray: E31458b

**Cornaceae**

- Cornus drummondii* C.A. Mey.: P27976s; E31364a; E31681b  
*Cornus racemosa* Lam.: P27490s

**Cucurbitaceae**

- Sicyos angulatus* L.: P28088s

**Cuscutaceae**

- Cuscuta campestris* Yuncker: P37100t

**Elaeagnaceae**

- \**Elaeagnus umbellata* Thunb.: P27336s; P36714a; E31654b

**Euphorbiaceae**

- Acalypha gracilens* Gray: S142s  
*Acalypha rhomboidea* Raf.: P27741s  
*Chamaesyce geyeri* (Engelm.) Small: P27956s; P36211a; E31491t  
*Chamaesyce maculata* (L.) Small: P28030s; P36174t; P37240b  
*Chamaesyce nutans* (Lag.) Small: P28047s  
\**Chamaesyce prostrata* (Ait.) Small: E31490t  
*Croton capitatus* Michx.: S354s  
*Croton glandulosus* L.: P27723s; P36218a; E31492t; E31837b  
*Crotonopsis linearis* Michx.: INAIa; E31493t; E31838b  
*Euphorbia corollata* L.: P27960s; E31366a; E31389t; E31459b  
\**Euphorbia esula* L.: P27314s  
*Poinsettia dentata* (Michx.) Kl. & Garcke: P28052s; P36193a; E31494t; E31839b

**Fabaceae**

- Amorpha canescens* Pursh: P27702s; E31367a; E31495t; E31460b  
*Amorpha fruticosa* L.: P27817s; P36184t  
*Amphicarpaea bracteata* (L.) Fern.: P28038s  
*Apios americana* Medic.: P28102s  
*Baptisia alba* (L.) Vent. E31390t  
\**Baptisia australis* (L.) R. Br.: P37106a  
*Crotalaria sagittalis* L.: P27962s  
*Dalea candida* (Michx.) Willd.: S322s  
*Dalea purpurea* Vent.: P27824s; E31368a; INAIt  
*Desmodium canadense* (L.) DC.: P28104s  
*Desmodium glutinosum* (Muhl.) A. Wood: P27842s  
*Desmodium illinoense* Gray: P27914s; E31840b  
\**Kummerowia stipulacea* (Maxim.) Makino: P28276s



*Lespedeza capitata* Michx.: P28122s; E31281a; E31254t; E37232b  
*Lespedeza intermedia* (S. Wats.) Britt.: P28567s  
\**Medicago lupulina* L.: P27413s; E30647a; E31682b  
\**Melilotus albus* Medic.: P27501s; E31369a; E31391t; E31461b  
\**Melilotus officinalis* (L.) Pallas: P27406s; E31706a; E30674a; E31683b  
\**Robinia pseudoacacia* L.: P27444s  
\**Securigera varia* (L.) Lassen: P27524s  
*Strophostyles helvula* (L.) Ell. var. *helvula*: P27933s; P36243a; E31841b  
*Strophostyles helvula* (L.) Ell. var. *missouriensis* (S. Wats.) Britt.: P27765s  
*Strophostyles leiosperma* (Torr. & Gray) Piper: P27925s  
*Tephrosia virginiana* (L.) Pers.: P27728s; E31282a; E31255t; E31462b  
\**Trifolium arvense* L.: P27747s  
\**Trifolium campestre* Schreb.: P27733s  
\**Trifolium hybridum* L.: P28455s  
\**Trifolium pratense* L.: P27473s; E31842b  
\**Trifolium repens* L.: P27474s  
\**Vicia villosa* Roth: P27476s

### **Fagaceae**

*Quercus alba* L.: P28443s  
*Quercus x bushii* Sarg.: E31634b  
*Quercus macrocarpa* Michx.: P27319s  
*Quercus marilandica* Muench.: E31655b  
*Quercus muhlenbergii* Englem.: P27475s  
*Quercus palustris* Muench.: P28094s  
*Quercus rubra* L.: P28042s  
*Quercus velutina* Lam.: P27187s; E30619a; E31256t; E31633b

### **Fumariaceae**

*Corydalis micrantha* (Engelm.) Gray: P27287s  
*Dicentra cucullaria* (L.) Bernh.: P27203s

### **Gentianaceae**

*Gentiana puberulenta* J. Pringle: INAI t

### **Geraniaceae**

*Geranium carolinianum* L.: P27553s; E31684b  
*Geranium maculatum* L.: P27329s

### **Grossulariaceae**

*Ribes missouriense* Nutt.: P27189s; P36227a; P36181t; E31636b

### **Haloragidaceae**

\**Myriophyllum spicatum* L.: P28260s

### **Hydrophyllaceae**

*Ellisia nyctelea* L.: P27278s  
*Hydrophyllum virginianum* L.: P27338s

### **Hypericaceae**

\**Hypericum perforatum* L.: P27700s  
*Hypericum punctatum* Lam.: P27996s  
*Hypericum sphaerocarpum* Michx.: P27797s

**Juglandaceae**

*Carya cordiformis* (Wangenh.) K. Koch: P27466s

*Carya ovata* (Mill.) K. Koch: P28119s

*Carya tomentosa* (Poir.) Nutt.: P28130s

*Juglans cinerea* L.: P28584s

*Juglans nigra* L.: P27291s

**Lamiaceae**

*Agastache nepetoides* (L.) Ktze.: P27944s

*Hedeoma hispida* Pursh: P27415s

\**Leonurus cardiaca* L.: P27708s; E31685b

*Lycopus americanus* Muhl.: P27955s

*Lycopus uniflorus* Michx.: P28079s

\**Mentha arvensis* L.: P27992s

*Monarda fistulosa* L. var. *fistulosa*: P27841s; E31843b

*Monarda fistulosa* L. var. *mollis* (L.) Benth.: P27950s

*Monarda punctata* L.: P27931s; E31283a; E31257t; E31844b

\**Nepeta cataria* L.: P27776s; P36164t; E31845b

*Physostegia virginiana* (L.) Benth.: P28078s

\**Prunella vulgaris* L.: P27967s

*Pycnanthemum virginianum* (L.) Dur. & B.D. Jacks.: P28098s

*Salvia azurea* Michx. & Lam.: P28060s

*Scutellaria lateriflora* L.: P28075s

*Scutellaria leonardii* Epling: P27837s

*Scutellaria ovata* Hill: P27744s

*Stachys hispida* Pursh: P28247s

*Stachys tenuifolia* Willd.: P27799s

*Teucrium canadense* L.: P27801s

*Trichostema dichotomum* L.: P27941s

**Linaceae**

*Linum sulcatum* Riddell: P27823s

**Lythraceae**

*Ammannia coccinea* Rottb.: P28237s

\**Lythrum salicaria* L.: P28249s

*Rotala ramosior* (L.) Koehne: P27866s

**Malvaceae**

*Callirhoe triangulata* (Leavenw.) Gray: P27762s; P36201a; E31496t; E31686b

*Hibiscus laevis* All.: P28075s

\**Malva neglecta* Wallr.: P28251s

**Menispermaceae**

*Menispermum canadense* L.: P27484s

**Molluginaceae**

\**Mollugo verticillata* L.: P27705s; P36219a; E31258t; E31687b

**Moraceae**

\**Morus alba* L.: P27285s; P36225a; E31259t

\**Morus tatarica* L.: E31688b

**Nelumbonaceae**

*Nelumbo lutea* (Willd.) Pers.: P28003s

**Nyctaginaceae**

*Mirabilis hirsuta* (Pursh) MacM.: P27793s

\**Mirabilis nyctaginea* (Michx.) MacM.: P27521s; E31370a; E31497t; E31689b

**Nymphaeaceae**

*Nymphaea tuberosa* Paine: P28263s

**Oleaceae**

*Fraxinus lanceolata* Borkh.: P27489s

*Fraxinus pennsylvanica* Marsh.: P36238a; P36165t

\**Syringa vulgaris* L.: P27321s

**Onagraceae**

*Circaea lutetiana* L.: P27709s

*Epilobium ciliatum* Raf.: P28438s

*Gaura longiflora* Spach: P28050s

*Oenothera biennis* L.: P28083s; P37102a

*Oenothera clelandii* W. Dietr., Raven, & W.L. Wagner: P27729s; P36205a; E31498t; E31463b

*Oenothera laciniata* Hill: P27926s

**Orobanchaceae**

*Orobanche fasciculata* Nutt.: G2634s

**Oxalidaceae**

*Oxalis stricta* L.: P27525s; E30648a

*Oxalis violacea* L.: E31637b

**Papaveraceae**

*Sanguinaria canadensis* L.: P27193s

**Phrymaceae**

*Phryma leptostachya* L.: P27844s

**Phytolaccaceae**

*Phytolacca americana* L.: S110s; E31846b

**Plantaginaceae**

*Plantago aristata* Michx.: P27758s

\**Plantago lanceolata* L.: P27735s

*Plantago patagonica* Jacq.: P27508s; E30649a; E30675t; E31690b

*Plantago rugelii* Decne.: P27840s

*Plantago virginica* L.: P27448s

**Polemoniaceae**

*Phlox divaricata* L.: P27194s

**Polygalaceae**

*Polygala polygama* Walt.: P27516s; E31285a; E30676t; E31464b

*Polygala sanguinea* L.: Observed at a.

*Polygala verticillata* L.: P22291s



**Polygonaceae**

- Antenoron virginianum* (L.) Roberty & Vautier: P28039s  
\**Fallopia convolvulus* (L.) A. Love: P27835s; E31691b  
*Fallopia scandens* (L.) Holub.: P28128s; E31499t  
*Persicaria amphibium* (L.) S.F. Gray: P28230s  
\**Persicaria cespitosa* (Blume) Nakai: P28068s  
\**Persicaria hydropiper* (L.) Opiz: P28093s  
*Persicaria lapathifolia* (L.) S.F. Gray: P28057s  
*Persicaria pensylvanica* (L.) Small: P27978s  
*Persicaria punctata* (Ell.) Small: P28056s  
\**Persicaria vulgaris* Webb & Moq.: P27979s  
*Polygonella articulata* (L.) Meisn.: P28220s; E31284a; E31260t  
\**Polygonum aviculare* L.: E31392t  
*Polygonum ramosissimum* Michx.: P28215s  
*Polygonum tenue* Michx.: P27930s; P36234a; P36171t; P37244b  
\**Rumex acetosella* L.: P27313s; E30650a; E30607t; E31656b  
*Rumex altissimus* Wood: P27540s  
\**Rumex crispus* L.: P27546s  
*Rumex verticillatus* L.: P27816s

**Portulacaceae**

- Claytonia virginica* L.: P27199s  
\**Portulaca oleracea* L.: P27865s  
*Talinum rugospermum* Holz.: P27740s; P36242a; P22637t; E31847b

**Primulaceae**

- Androsace occidentalis* Pursh: P27157s; E31329a; E31315t; E31657b  
*Lysimachia ciliata* L.: P27798s

**Ranunculaceae**

- Anemone canadensis* L.: P27317s  
*Anemone caroliniana* Walt.: P27155s; INA1a  
*Anemone cylindrica* Gray: P27538s; INA1a  
*Anemone quinquefolia* L.: P27202s  
*Anemone virginiana* L.: P27790s  
*Aquilegia canadensis* L.: P27286s  
*Caltha palustris* L.: P27316s  
*Clematis virginiana* L.: P28273s  
*Ranunculus abortivus* L.: P27168s; E30677t  
*Ranunculus fascicularis* Bigel.: P27301s  
*Ranunculus pensylvanicus* L.f.: P27972s  
*Ranunculus septentrionalis* Poir.: P27330s  
*Thalictrum dasycarpum* Fisch. & Lall.: P27802s

**Rhamnaceae**

- Ceanothus americanus* L.: P27731s; P36199a; INA1t  
*Ceanothus herbaceus* Raf.: P27458s  
\**Rhamnus cathartica* L.: P27328s

**Rosaceae**

- Agrimonia gryposepala* Wallr.: P27965s  
*Agrimonia pubescens* Wallr.: P28002s  
*Crataegus calpodendron* (Ehrh.) Medic.: P27985s

*Fragaria virginiana* Duchesne: P27294s  
*Geum canadense* Jacq.: P27710s; E31500t  
*Geum triflorum* Pursh: P27153s  
*Malus coronaria* (L.) Mill.: P27174s  
*Malus ioensis* (Wood) Britt.: P27276s  
\**Malus pumila* Mill.: P27205s  
*Physocarpus opulifolius* (L.) Maxim.: P28004s  
\**Potentilla argentea* L.: P27297s  
*Potentilla arguta* Pursh: INAIIt  
\**Potentilla inclinata* Vill.: P27405s  
*Potentilla norvegica* L.: P27754s  
\**Potentilla recta* L.: P27504s; E31371a; E30678t; E31692b  
*Potentilla simplex* Michx.: P28602s; INAIIt  
*Prunus americana* Marsh.: P27162s  
*Prunus nigra* Ait.: P27160s  
*Prunus serotina* Ehrh.: P27341s; E30620a; E31318t; E31658b  
*Prunus susquehanae* Willd.: INAIa; E31316t  
*Prunus virginiana* L.: P28296s; P36229a; E31317t  
*Rosa carolina* L.: P27506s; P37105a; E31393t  
\**Rosa multiflora* Thunb.: P27545s; P36712a  
*Rosa suffulta* Greene: P28100s  
*Rubus allegheniensis* Porter: P27536s  
*Rubus argutus* Link: P27477s  
*Rubus baileyanus* Britt.: E31394t  
*Rubus flagellaris* Willd.: P27445s  
*Rubus occidentalis* L.: P27461s; P36228a; P36163t; E31693b  
*Rubus pensilvanicus* Poir.: E31848b

### **Rubiaceae**

*Cephalanthus occidentalis* L.: P27807s  
*Diodia teres* Walt.: P27937s; P36239a; E31261t; E31849b  
*Galium aparine* L.: P27288s; E30679t; E31694b  
*Galium circaezans* Michx.: P28579s  
*Galium concinnum* Torr. & Gray: P27843s  
*Galium triflorum* Michx.: P27743s

### **Rutaceae**

*Ptelea trifoliata* L.: P27750s; INAIa; E30680t  
*Zanthoxylum americanum* Mill.: P27173s; E31372a

### **Salicaceae**

*Populus deltoides* Marsh.: P27340s; P36711a  
*Populus grandidentata* Michx.: P27333s  
*Populus tremuloides* Michx.: P27961s  
*Salix amygdaloides* Anderss.: P27804s  
*Salix interior* Rowlee: P27206s  
*Salix nigra* Marsh.: P27318s

### **Santalaceae**

*Comandra umbellata* (L.) Nutt.: P27335s; INAIIt

### **Saxifragaceae**

*Penthorum sedoides* L.: P27973s

**Scrophulariaceae**

*Agalinis tenuifolia* (Vahl) Raf.: P28451s

*Aureolaria grandiflora* (Benth.) Pennell: S216s

*Bacopa rotundifolia* (Michx.) Wettst.: P27971s

*Besseyia bullii* (Eat.) Rydb.: P27539s; E31659b

\**Chaenorrhinum minus* (L.) Lange: P 27854s

*Gratiola neglecta* Torr.: P27549s

\**Linaria vulgaris* Mill.: P27795s

*Lindernia dubia* (L.) Pennell var. *dubia*: P29046s

*Mimulus ringens* L.: P28089s

*Nuttallanthus canadensis* (L.) D. Sutton: P27178s; E30621a; E30608t; E31660b

*Penstemon grandiflorus* Nutt.: P36188t; P37247b

*Penstemon pallidus* Small: P27325s; E30651a; E30609t; E31695b

*Scrophularia lanceolata* Pursh: P27446s

\**Verbascum blattaria* L.: P27953s

\**Verbascum thapsus* L.: P27995s; E31707a; E31501t; E31850b

\**Veronica arvensis* L.: P27298s; E30622a; E30682t; E31661b

\**Veronica dillenii* Crantz: P27180s

*Veronica peregrina* L.: P27282s

*Veronicastrum virginicum* (L.) Farw.: INAIIt

**Solanaceae**

*Physalis heterophylla* Nees: P27515s; E31373a; E31502t; E31851b

*Physalis subglabrata* Mack. & Bush: P28236s; E31465b

*Physalis virginiana* Mill.: P27459s; E31374a; P36186t; E31696b

*Solanum carolinense* L.: P27724s; P37101t; E31697b

\**Solanum dulcamara* L.: P36237a; E30681t

*Solanum ptychanthum* Dunal: P27745s; E31503t

\**Solanum rostratum* Dunal: P28031s

**Tiliaceae**

*Tilia americana* L.: P27443s

**Ulmaceae**

*Celtis occidentalis* L.: P27172s; P37103a; E31505t

*Ulmus americana* L.: P27167s; P36200a

\**Ulmus pumila* L.: P27152s; E31504t; E31698b

*Ulmus rubra* Muhl.: P27196s

**Urticaceae**

*Boehmeria cylindrica* (L.) Sw.: P28007s

*Laportea canadensis* (L.) Wedd.: P28082s

*Parietaria pensylvanica* Muhl.: P27455s; E31852b

*Pilea pumila* (L.) Gray: P28272s

*Urtica gracilis* Ait.: P27748s

**Verbenaceae**

*Phyla lanceolata* (Michx.) Greene: P27839s

*Verbena bracteata* Lag. & Rodr.: P27734s; E31375a

*Verbena hastata* L.: P28055s

*Verbena stricta* Vent.: P27869s; E31286a; E31262t; E31466b

*Verbena urticifolia* L.: P27808s



**Violaceae**

*Viola pedata* L.: P27186s; E30623a; E31319t; E31662b

*Viola pratincola* Greene: P27327s; P37097t

*Viola pubescens* Ait.: P27339s

\**Viola rafinesquii* Greene: P27322s; E30610t; E31663b

*Viola sororia* Willd.: P27185s

**Vitaceae**

*Parthenocissus inserta* (Kern.) K. Fritsch: P27811s; E31853b

*Parthenocissus quinquefolia* (L.) Planch.: P27939s; P36226a; E31506t

*Vitis riparia* Michx.: P27447s; P36236a; E31395t; E31854b



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